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Effects of heat stress on the quality of *Trichogrammatoidea bactrae* Nagaraja (Hymenoptera: Trichogrammatidae)

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Abstract

Trichogrammatoidea bactrae Nagaraja (Hymenoptera: Trichogrammatidae) is an important natural enemy of many species of lepidopterous pests. The effects of heat stress temperature (33, 36, and 39°C), duration of exposure (2, 4, 6, and 8 h), and developmental stage during exposure (embryo-first instar larvae, second instar larvae, prepupae, and pupae) on the development and reproduction of parasitoid *T. bactrae* were investigated in the laboratory. When exposed to 39°C for 8 h during pupal stage, only 19.90% adults emerged from host eggs, and more than 14% were deformed (wings were folded or incomplete). Parasitoid females exposed to 39°C for 8 h as prepupae only lived for 1.45 days and parasitized about 23.5 host eggs. Moreover, life-table parameters of *T. bactrae* were also influenced by exposure to heat stress temperatures during each preimaginal developmental stage. Based on these results, we propose that *T. bactrae* is susceptible to high temperatures, especially at 39°C. Thus, this parasitoid may be more effectively controlling lepidopterous pests during cooler weather conditions.

Keywords: heat stress, *Trichogrammatoidea bactrae*, deformed wings, reproduction, life-table parameter

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Introduction

Ambient temperature is an important factor influencing many aspects of insect ecology and development. It is clear that the change in global climate includes not only an increase in average temperatures, but also a high frequency of extreme climatic events such as heat waves (Easterling *et al.*, 2000; Hansen *et al.*, 2012). Extreme temperatures are highly stressful and are known to have detrimental effects on insects (Rinehart *et al.*, 2000; Malmendal *et al.*, 2006; Hance *et al.*, 2007; Terblanche *et al.*, 2011; Hoffmann *et al.*, 2013). High temperatures threaten the survival of insects on a daily basis (Rinehart *et al.*, 2000). Mortality may occur immediately for several insects of economic importance (Armstrong, 1992; Hansen, 1992), or may result in a failure to complete development (Denlinger *et al.*, 1991). In addition, insects that survive heat stress may pay a price manifested in their life history traits (Chihrane *et al.*, 1993; Krebs & Loeschcke, 1994; Chihrane & Laugé, 1996; Rinehart *et al.*, 2000; Ma *et al.*, 2003; Mahroof *et al.*, 2005*a*; Jørgensen *et al.*, 2006; Sisodia & Singh, 2006; Cui *et al.*, 2008; Xie *et al.*, 2008). Furthermore, heat stress in adults can also influence their offspring, reducing the rate of egg hatching (Silbermann & Tatar, 2000), or inducing changes in morphology (Andersen *et al.*, 2005).

Parasitoids are likely extremely susceptible to changes in environmental conditions, as they rely on a series of adaptations to the ecology and physiology of their hosts for survival (Hance *et al.*, 2007). Generally, the success of using parasitoids as biological control agents relies not only on the time and the numbers of parasitoids released, but also on their quality (longevity and fecundity) (Dutton *et al.*, 1996).

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Therefore, the ability of a parasitoid to tolerate the physical environment is a critical factor in evaluating their biological control potential (Tillman & Powell, 1991; Miller & Gerth, 1994). *Trichogrammatoidea bactrae* Nagaraja (Hymenoptera: Trichogrammatidae) is an important natural enemy of many species of lepidopterous pests (Lin, 1994). This parasitoid is mostly found in many tropical and subtropical countries, such as India, Malaysia, Thailand, Pakistan, Australia, and can also be encountered in some provinces of China (i.e., Guangdong, Hainan, Fujian and Taiwan) (Lin, 1994; Huang *et al.*, 2002; Liu *et al.*, 2004; Tian & Lin, 2009). Many studies showed that *T. bactrae* has great parasitization potential on eggs of the diamondback moth, *Plutella xylostella* (Hübner) (Wuhrer & Hassan, 1993; Vasquez *et al.*, 1997; Guo *et al.*, 1999); thus, this parasitoid is considered as a suitable candidate to control the diamondback moth. It is necessary and important to estimate the efficacy of this parasitoid under field conditions, where temperature conditions can be subjected to daily variations.

In a recent study, *T. bactrae* were exposed to an increasing range of constant temperatures during their development and their fitness parameters were assessed. Chen *et al.* (2005) reported that the minimum and maximum temperatures for *T. bactrae* development were 11.9 and 38.95°C, respectively. Nadeem & Hamed (2008) described that only 36.1% adult *T. bactrae* emerged successfully from host eggs at 35°C. However, the effects of heat stress on this parasitoid have not been reported yet.

The goal of this study was to measure the effects of heat stress on biological parameters (emergence percentage and deformity rate of adults, longevity and fecundity of surviving females, and life-table parameters) of *T. bactrae*, under conditions simulating high temperatures of field microclimate, in order to make some realistic recommendations for field applications of this parasitoid.

Materials and methods

Insect origin and rearing

T. bactrae were reared from parasitized diamondback moth egg masses (about 100 eggs) collected in May 2011 from Chinese Kale (*Brassica alboglabra* Bailey) fields located near Guangzhou, China. The stock population (about 20,000 parasitoids) was maintained and reared on eggs of *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) in glass tubes (2.3 cm internal diameter, 7.4 cm internal height) at 25 ± 1°C, 80 ± 5% R.H. and a 14L:10D photoperiod in the laboratory. These rearing conditions of the parasitoids were as the 'control conditions' throughout our study. The eggs of *C. cephalonica* (approximately 2000 eggs) were stuck to 3 × 2 cm cardboard strip and exposed to UV light (30 W) for 30 min before experiments and rearing of *T. bactrae*. *C. cephalonica* was reared following the procedure described in Wang *et al.* (2012). To feed the adults of *T. bactrae*, a droplet of 25% honey solution was placed in the glass tube prior to or upon their emergence.

To obtain standardized parasitoids for experiments, approximately 150 fed, newly emerged (< 6 h after emergence) and mated females of *T. bactrae* were supplied with fresh host eggs (approximately 2000 eggs) on cardboard strip (3 × 2 cm). After 8 h, parasitoids were removed with a brush from the egg card. Then the card was cut into small egg sheets (1 × 0.5 cm, about 160 eggs of *C. cephalonica* per sheet), inserted into small glass vials (1 cm internal diameter, 5.5 cm internal height) and maintained under control conditions. The entrances of the glass vials were closed with cotton balls to allow air circulation and to prevent the escaping of wasps.

Experimental design

The experiment was designed to test three factors: heat stress temperature, developmental stage of parasitoids exposed to high temperature, and duration of exposure.

Heat stress was applied to the four preimaginal developmental stages: embryo-first instar larvae (24 h after egg laying), second instar larvae (48 h after egg laying), prepupae (96 h after egg laying), and pupae (144 h after egg laying) (Chen *et al.*, 2004).

To test the resistance of *T. bactrae* to heat stress, we used climatic temperature controlled cabinets (Ningbo Jiangnan RXZ-380A, Ningbo, Zhejiang Province, China). The temperatures (33, 36, and 39°C) were chosen based on the field microclimate temperatures (recorded by a hygrothermograph (Smartsensor AR847, HongKong, China) in preliminary experiments) in Southern China during summer months. The exposure times (2, 4, 6, and 8 h) were selected, in order to simulate the theoretical duration of extreme temperatures. Parasitoids maintained continuously at 25°C, 80 ± 5% R.H. and a 14L:10D photoperiod served as controls.

Measured traits

Development aspects

In order to test the effects of heat stress on survival and development of *T. bactrae*, we calculated the emergence percentage and deformity rate of adults. After each heat exposure, egg sheets were placed at 25°C as described above. Emergence percentage and deformity rates of adults were measured after the parasitoids completely emerged from host eggs. Emergence was defined as empty eggs with eclosion hole on them. We considered adults as deformed when their wings were folded or incomplete. Ten replicates were carried out for each treatment.

The general linear model (GLM) procedure (SPSS 13.0, SPSS Inc., Chicago, IL) with interaction terms was used to analyze the effects of heat stress temperature (33, 36, and 39°C), developmental stage of parasitoids exposed to high temperature (embryo-first instar larvae, second instar larvae, prepupae, or pupae), duration of exposure (2, 4, 6, or 8 h) and all their interactions on the emergence percentage and deformity rate of *T. bactrae* adults subjected to heat stress. Under the condition of the same developmental stage and same temperature, the variability of the emergence percentage and deformity rate as functions of the heat stress duration were analyzed assuming a GLM. When statistical differences existed between data sets ($P < 0.05$), Tukey's HSD test was used to determine statistically significant differences between means.

Reproduction aspects

To determine the effects of heat stress on reproduction of *T. bactrae*, the life-table method of the surviving parasitoids (Chen *et al.*, 2005; Wang *et al.*, 2012) was applied. After heat exposure, egg sheets of parasitoids were maintained in the small glass vials under control conditions. Five replicates (egg sheets) were carried out for each treatment.

After the parasitoids emerged, they were fed a 25% honey solution and were placed under control conditions for 2 h to mate. The surviving and mated female parasitoids were introduced individually into a clean glass tube, and supplied with a 25% honey solution on the internal wall as food. As previously described, tubes were closed with cotton balls. For each treatment, 20 surviving females were randomly selected from the five replicates to further investigate the longevity and fecundity of surviving female adults, as well as the daily daughter output. To determine the fecundity of each female parasitoid an egg sheet (1 × 0.5 cm) with about 160 *C. cephalonica* eggs stuck to cardboard strips was inserted into each tube, and was replaced with a new egg sheet after 24 h and substituted daily until all individuals had died. Survival of females was recorded daily, and honey solution was added when necessary. The egg sheets were labeled and placed into small glass vials and incubated for 13 days under control conditions, long enough for complete emergence of offspring from the initial parasitism. Finally, the vials were placed into −10°C for 1 h to kill offspring, and the number of parasitized eggs (black), and daughters were recorded for each treatment under a dissecting microscope (Zeiss Stemi 2000-CS, Shanghai, China).

Daily schedules of survival rate and fecundity were integrated into a life-table format (Dastjerdi *et al.*, 2009; Bayram *et al.*, 2010) and used to estimate life-table parameters: probability of an individual surviving to age x (l_x), the number of daughters produced by a female at age x (m_x), net reproduction rate ($R_0 = \Sigma l_x m_x$), mean generation time ($T = \Sigma x l_x m_x / \Sigma l_x m_x$), intrinsic rate of natural increase ($r_m = \ln R_0 / T$), finite rate of increase ($\lambda = e^{rm}$), and doubling time ($DT = \ln 2 / r_m$).

The effects of heat stress temperature, developmental stage of parasitoids exposed to high temperature, duration of exposure and their interactions with each response variable (longevity and fecundity of female adults and life-table parameters of *T. bactrae*) were analyzed using GLM as the model (SPSS 13.0, SPSS Inc., Chicago, IL). For the same developmental stage and temperature, GLM was used to analyze the effect of different duration of exposure on each response variable. Means were compared using Tukey's HSD test with $\alpha = 0.05$.

Results

Effects of heat stress on the development of T. bactrae

Emergence rate of *T. bactrae* adults was remarkably affected by the developmental stage at the time of heat stress, heat stress temperature, duration of exposure, and all the possible interactions of these three factors (table 1). After heat stress, the emergence rate of *T. bactrae* adults decreased with the increase in exposure time (fig. 1). Only 19.90% adults emerged after they had been exposed to 39°C for 8 h during pupal stage (fig. 1D). Compared with other developmental stages, significantly fewer adults emerged if they had been exposed to heat stress at the embryo-first instar larval stage ($P < 0.05$, Tukey's HSD test).

All three factors, developmental stage during heat stress, heat stress temperature and exposure time, and their interactions had significant effects on the deformity rate of *T. bactrae* adults (table 1). The deformity rate was significantly higher when the wasps were heat stressed during pupal stage compared to any other stage. And more than 14% adults emerged with abnormal wings when they were exposed as pupae to 39°C for 6 or 8 h (fig. 2D).

Table 1. Three-factor ANOVA statistics for analyzing emergence and deformity rate of *T. bactrae* adults, the mean longevity and fecundity of females treated by heat stress.

Indexes	Factors	df	*F*	*P*
Emergence rate	a	3, 539	10.72	<0.001
	b	2, 539	356.569	<0.001
	c	4, 539	205.848	<0.001
	a*b	6, 539	13.999	<0.001
	a*c	12, 539	4.37	<0.001
	b*c	8, 539	55.018	<0.001
	a*b*c	24, 539	4.142	<0.001
Deformity rate	a	3, 537	16.452	<0.001
	b	2, 537	20.194	<0.001
	c	4, 537	13.7	<0.001
	a*b	6, 537	3.648	0.001
	a*c	12, 537	1.848	0.038
	b*c	8, 537	5.288	<0.001
	a*b*c	24, 537	1.694	0.021
Mean longevity	a	3, 1140	7.96	<0.001
	b	2, 1140	123.081	<0.001
	c	4, 1140	50.493	<0.001
	a*b	6,1140	2.979	0.007
	a*c	12, 1140	2.342	0.006
	b*c	8, 1140	10.276	<0.001
	a*b*c	24, 1140	1.476	0.065
Fecundity	a	3, 1140	3.868	0.009
	b	2, 1140	145.823	<0.001
	c	4, 1140	52.196	<0.001
	a*b	6, 1140	2.066	0.055
	a*c	12, 1140	1.587	0.089
	b*c	8, 1140	11.766	<0.001
	a*b*c	24, 1140	1.240	0.196

a: developmental stage of parasitoids exposed to high temperature; b: heat stress temperature; c: duration of exposure.

Effects of heat stress on the reproduction of T. bactrae

The mean longevity of *T. bactrae* females was negatively influenced by developmental stage during heat stress, heat stress temperature, duration of exposure, and all the possible interactions between these three factors, except for the triple interaction of developmental stage, heat stress temperature, and duration of exposure (table 1). After heat stress during each preimaginal developmental stage, the longevity of females was reduced when compared to control condition. Furthermore, compared to other heat stress temperatures, exposure to 39°C significantly reduced longevity of *T. bactrae* females (fig. 3). In comparison with their longevity at other treatment stages, females exposed as prepupae to heat stress lived significantly shorter ($P < 0.05$, Tukey's HSD test). In particular, females exposed as prepupae to 39°C for 8 h lived for only 1.45 days (fig. 3C).

The mean fecundity of *T. bactrae* females was negatively affected by the developmental stage of heat stress, heat stress temperature, duration of exposure, and the temperature in interaction with the duration of heat stress (table 1). When exposed to 39°C during each preimaginal developmental stage, emerged females parasitized fewer eggs than untreated ones (fig. 4). Moreover, females exposed as prepupae to 39°C for 8 h only parasitized on average 23.5 eggs in their lifetime

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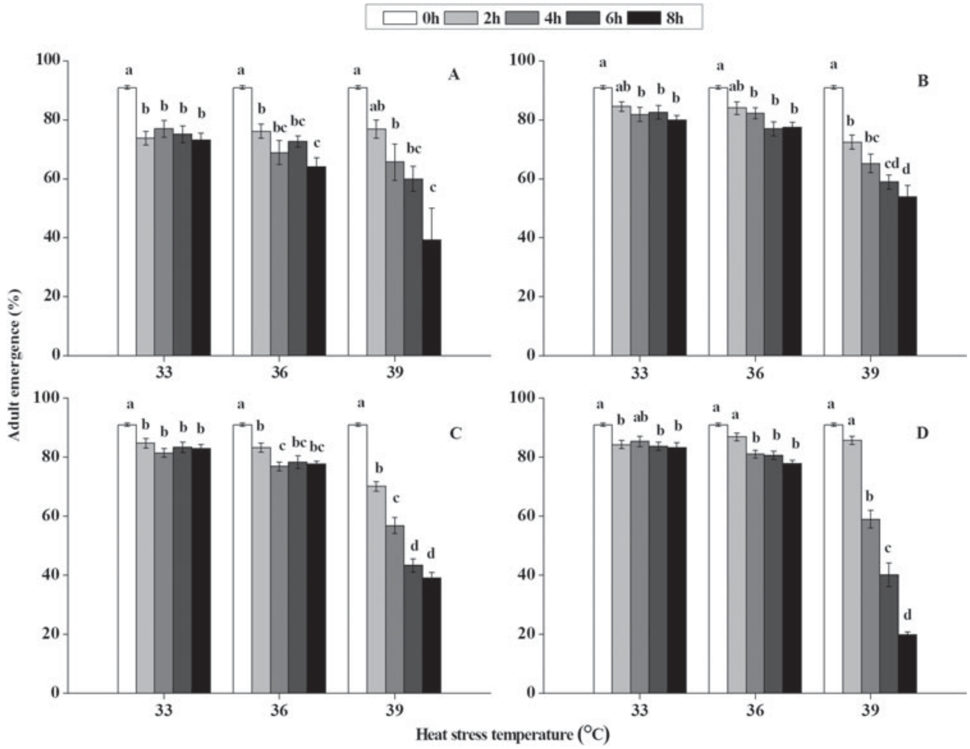

Fig. 1. Emergence rate (%) of *T. bactrae* adults from heat treated stage (A: embryo-first instar larvae; B: second instar larvae; C: prepupae; or D: pupae). Under similar temperature and developmental stage conditions, only if statistically significant differences between data sets of different exposure times were detected ($P > 0.05$), subsequent multiple comparisons were performed. Different letters in different durations of exposure denote statistically significant differences ($P < 0.05$, Tukey's HSD test), the same below.

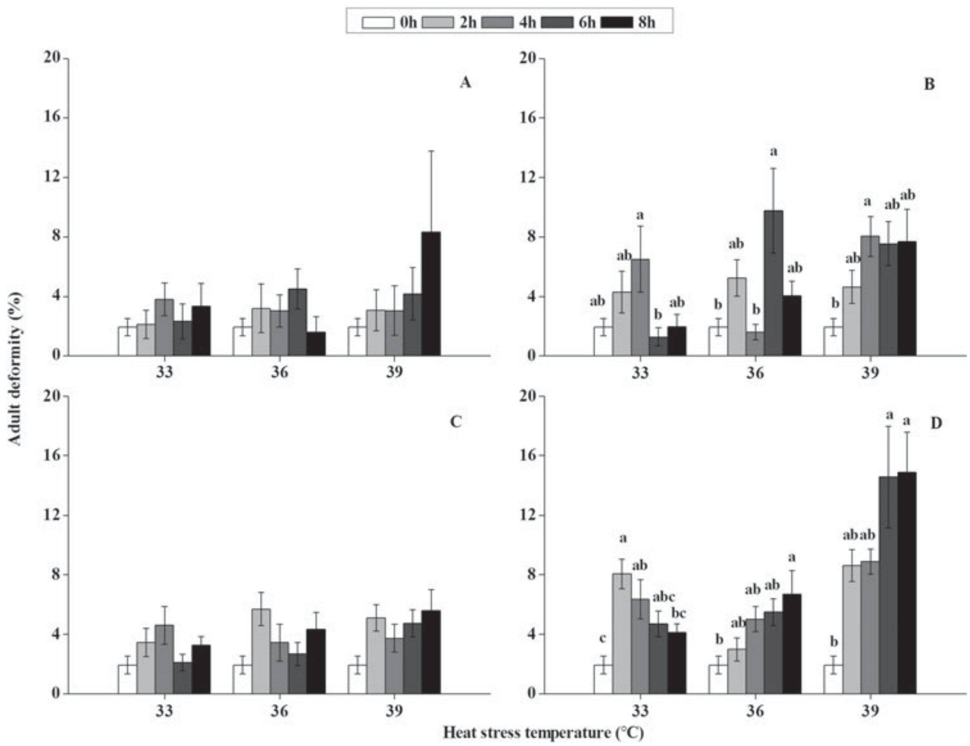

Fig. 2. Deformity rate (%) of *T. bactrae* adults that emerged from treated stage (A: embryo-first instar larvae; B: second instar larvae; C: prepupae; or D: pupae).

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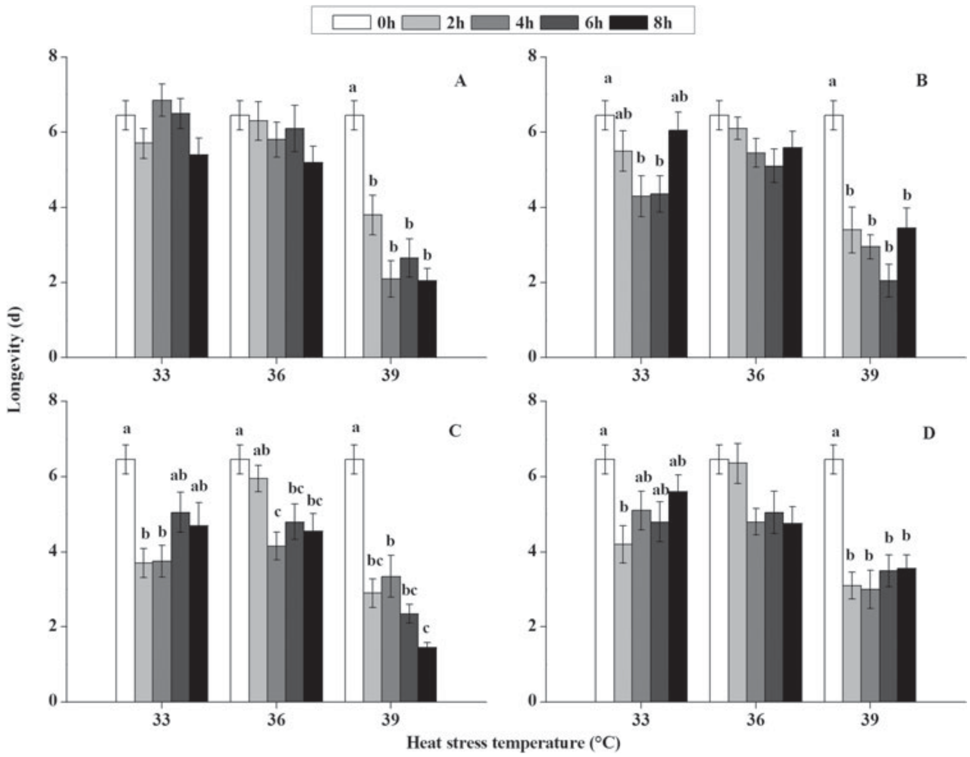

Fig. 3. Mean longevity (days) of *T. bactrae* females that emerged from treated stage (A: embryo-first instar larvae; B: second instar larvae; C: prepupae; or D: pupae).

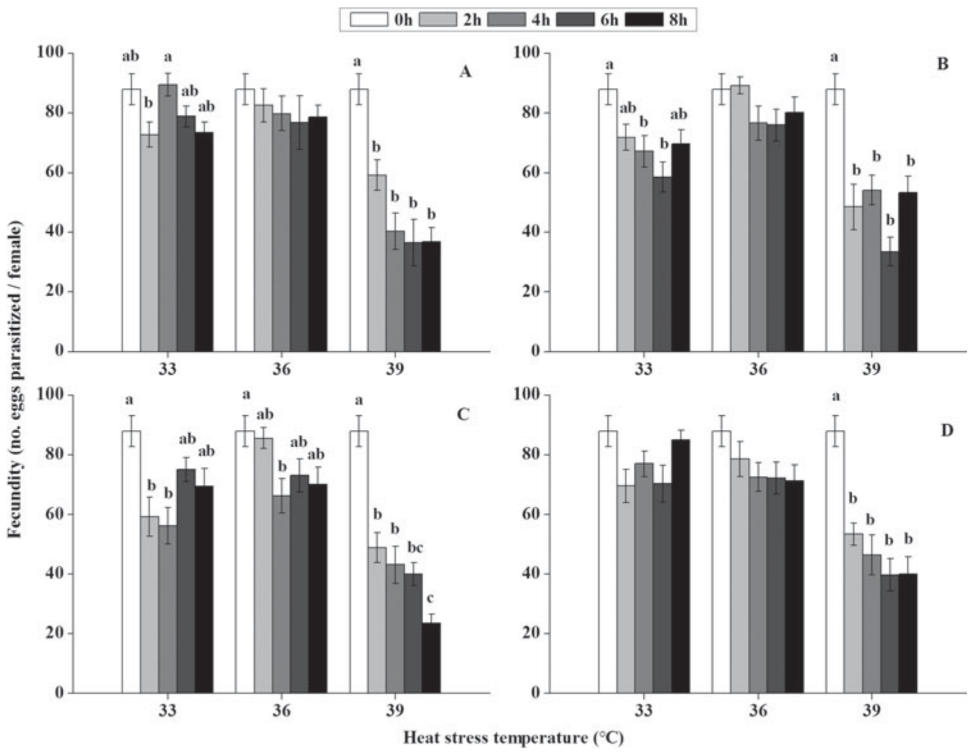

Fig. 4. Fecundity (no. eggs parasitized) of *T. bactrae* females that emerged from treated stage (A: embryo-first instar larvae; B: second instar larvae; C: prepupae; or D: pupae).

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Table 2. Three-factor ANOVA statistics for analyzing life-table parameters of *T. bactrae* treated by heat stress.

Indexes	Factors	df	F	P
R_0	a	3, 1140	0.022	0.996
	b	2, 1140	76.269	<0.001
	c	4, 1140	91.961	<0.001
	a*b	6, 1140	2.203	0.041
	a*c	12, 1140	1.982	0.023
	b*c	8, 1140	7.967	<0.001
	a*b*c	24, 1140	1.483	0.063
r_m	a	3, 1023	3.484	0.015
	b	2, 1023	76.116	<0.001
	c	4, 1023	39.677	<0.001
	a*b	6, 1023	4.23	<0.001
	a*c	12, 1023	1.859	0.036
	b*c	8, 1023	12.609	<0.001
	a*b*c	24, 1023	1.523	0.051
λ	a	3, 1023	3.296	0.02
	b	2, 1023	81.75	<0.001
	c	4, 1023	42.874	<0.001
	a*b	6, 1023	4.286	<0.001
	a*c	12, 1023	1.868	0.034
	b*c	8, 1023	13.159	<0.001
	a*b*c	24, 1023	1.536	0.048
T	a	3, 1023	3.099	0.026
	b	2, 1023	64.91	<0.001
	c	4, 1023	55.408	<0.001
	a*b	6, 1023	2.438	0.024
	a*c	12, 1023	1.453	0.136
	b*c	8, 1023	6.087	<0.001
	a*b*c	24, 1023	0.901	0.601
DT	a	3, 1019	2.844	0.037
	b	2, 1019	31.566	<0.001
	c	4, 1019	17.236	<0.001
	a*b	6, 1019	2.739	0.012
	a*c	12, 1019	1.616	0.081
	b*c	8, 1019	7.763	<0.001
	a*b*c	24, 1019	1.119	0.315

a: developmental stage of parasitoids exposed to high temperature; b: heat stress temperature; c: duration of exposure.

(fig. 4C). In addition, the parasitic ability of females was also significantly influenced by exposure to 33°C during embryo-first instar larval or second instar larval or prepupal stage, 36°C during prepupal stage (fig. 4A–C). Fewer eggs were parasitized when females were heat stressed during prepupal stage compared to all other stages ($P<0.05$, Tukey's HSD test).

Effects of heat stress on the life-table parameters of T. bactrae

Both heat stress temperature and duration of exposure had significant effects on R_0 (net reproduction rate) and r_m (intrinsic rate of natural increase) of *T. bactrae*, as did the possible double interactions of developmental stage, heat stress temperature, and duration of exposure. Developmental stage had a statistically significant effect on r_m but not on R_0. All three factors, developmental stage during heat stress, heat stress temperature and duration of exposure had significant influences on λ (finite rate of increase) of *T. bactrae*, as did the possible interactions among them. The T (mean generation time) and DT (doubling time) of *T. bactrae* were significant affected by developmental stage of heat stress, heat stress temperature, duration of exposure, and all the possible double interactions among them, except for the interaction of developmental stage and duration of exposure (table 2).

After heat stress, R_0, r_m and λ were lower than untreated parasitoids, and this tendency was especially pronounced for exposure to 39°C during each preimaginal developmental stage. In addition, heat stress treatment can shorten the mean generation time and increase the doubling time of *T. bactrae* (table 3).

Discussion

Our results show that all the preimaginal developmental stages of *T. bactrae* are susceptible to heat stress. This susceptibility manifests itself in a reduction in emergence rate, longevity, and fecundity, as well as an increase of adult malformation incidences. In addition, heat sensitivity was enhanced as heat stress temperatures increased.

Generally, high temperature can affect emergence of parasitoids (Chihrane *et al.*, 1993; Liu & Tsai, 2002). After heat stress, the emergence rate of *T. bactrae* adults decreased with the increase in exposure time, especially when parasitoids were exposed to 39°C. After exposure to 39°C for 8 h during pupal stage, the emergence rate was only 19.90%, and more than 14% adults were deformed. Insects are especially vulnerable to desiccation during the pupal stage since they are close to adult molt (Chihrane *et al.*, 1993). Female parasitoids with abnormal wings will not fly normally, in which case they would have little chance to encounter food or host eggs. Thus, heat stress is bound to result in reduced survival and parasitic (or reproductive) ability of female parasitoids.

Our study shows that preimaginal heat stress is harmful to the survival of *T. bactrae* females. The mean life span of *T. bactrae* females that survive heat stress was shortened; in particular females exposed as prepupae to 39°C for 8 h survived only for 1.45 days (fig. 1). Similar results have previously been reported for *Trichogramma brassicae* females where heat stress treatment during pupal stage decreased their mean survival rates (Chihrane *et al.*, 1993; Chihrane & Laugé, 1996). However, when adult parasitoid of *Aphidius ervi* was exposed to high temperatures, the mean life span of surviving wasps was also reduced (Ismaeil *et al.*, 2013). Insect metabolic rate depends on temperature which influences their longevity so that insects live for a shorter time under the condition of higher temperatures (Denlinger & Yocum, 1998; Speight *et al.*, 1999). Thus, the negative effect of heat stress on the longevity of *T. bactrae* females is likely to be due to immediate and direct effects of short-term high temperature on their physiology.

Heat stress not only influenced the survival of female parasitoids but also decreased their fecundity. Many studies reported that high temperatures can interrupt the normal functioning of the reproductive system in both sexes of insects (Arbogast, 1981; Saxena *et al.*, 1992; Mahroof *et al.*, 2005*b*). In our study, *T. bactrae* females that emerged from each treatment parasitized fewer eggs than untreated ones. Females exposed as prepupae to 39°C for 8 h only parasitized 23.5 eggs per female in their lifetime compared to 87.9 in the control treatment (fig. 4). Similar results were reported by Roux *et al.* (2010): after exposure to 36°C for 1 h, the surviving females of *A. avenae* laid fewer eggs. The reduction in fecundity may be due to the direct cost of heat stress as reported for *Drosophila melanogaster* and for the parasitoid *Trichogramma carverae* (Krebs & Loeschcke, 1994; Scott *et al.*, 1997), alternatively

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Table 3. Life-table parameters of *T. bactrae* after exposure to heat stress treatments.

Tem. (°C)	Duration of exposure (h)	Embryo-first instar larval					Second instar larval				
		R_0	r_m	λ	T	DT	R_0	r_m	λ	T	DT
(a)											
33	0[1]	59.80 ± 3.63a[2]	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1	1.9 ± 0.0	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0b
	2	39.15 ± 3.99b	0.33 ± 0.01b	1.39 ± 0.01b	11.0 ± 0.1	2.2 ± 0.1	39.40 ± 3.42b	0.34 ± 0.01ab	1.40 ± 0.01ab	11.0 ± 0.1b	2.1 ± 0.0ab
	4	40.20 ± 5.41b	0.35 ± 0.01ab	1.42 ± 0.01ab	11.1 ± 0.1	2.0 ± 0.0	41.80 ± 3.03b	0.34 ± 0.01ab	1.41 ± 0.01ab	10.8 ± 0.1b	2.1 ± 0.1ab
	6	43.90 ± 3.37ab	0.34 ± 0.01ab	1.40 ± 0.01ab	11.3 ± 0.1	2.1 ± 0.0	32.90 ± 3.95b	0.32 ± 0.01b	1.38 ± 0.01b	10.9 ± 0.1b	2.2 ± 0.1a
	8	41.50 ± 4.37b	0.34 ± 0.01ab	1.41 ± 0.01ab	11.0 ± 0.1	2.1 ± 0.1	28.95 ± 4.25b	0.33 ± 0.01b	1.39 ± 0.01b	11.1 ± 0.1ab	2.1 ± 0.0ab
36	0	59.80 ± 3.63[3]	0.36 ± 0.00	1.43 ± 0.01	11.3 ± 0.1	1.9 ± 0.0	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1	1.9 ± 0.0b
	2	42.95 ± 4.92	0.35 ± 0.01	1.42 ± 0.01	11.1 ± 0.1	2.0 ± 0.0	58.60 ± 1.75a	0.36 ± 0.00a	1.44 ± 0.01a	11.3 ± 0.1	1.9 ± 0.0b
	4	44.35 ± 5.84	0.36 ± 0.01	1.43 ± 0.01	11.2 ± 0.1	2.0 ± 0.0	43.20 ± 5.14ab	0.35 ± 0.01ab	1.42 ± 0.01ab	11.1 ± 0.1	2.0 ± 0.0ab
	6	42.30 ± 6.02	0.32 ± 0.02	1.38 ± 0.03	11.2 ± 0.1	2.1 ± 0.1	32.70 ± 6.16b	0.33 ± 0.01b	1.39 ± 0.02b	11.1 ± 0.1	2.2 ± 0.1a
	8	47.15 ± 4.17	0.34 ± 0.01	1.41 ± 0.01	11.2 ± 0.1	2.0 ± 0.0	38.60 ± 6.08b	0.36 ± 0.00ab	1.43 ± 0.01ab	11.2 ± 0.1	2.0 ± 0.0b
39	0	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0c	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0c
	2	33.30 ± 3.09b	0.33 ± 0.01ab	1.39 ± 0.01ab	10.7 ± 0.1b	2.2 ± 0.0bc	32.45 ± 4.79b	0.33 ± 0.01ab	1.39 ± 0.01ab	10.9 ± 0.2b	2.1 ± 0.0bc
	4	19.70 ± 3.32c	0.27 ± 0.02bc	1.31 ± 0.02bc	10.6 ± 0.1b	2.5 ± 0.1abc	29.75 ± 3.39bc	0.31 ± 0.01bc	1.37 ± 0.01bc	10.7 ± 0.1b	2.3 ± 0.1ab
	6	18.00 ± 3.65c	0.26 ± 0.02bc	1.30 ± 0.03c	10.7 ± 0.1b	2.7 ± 0.3ab	15.55 ± 3.30c	0.30 ± 0.01c	1.35 ± 0.01c	10.7 ± 0.1b	2.3 ± 0.1a
	8	9.65 ± 2.89c	0.25 ± 0.03c	1.29 ± 0.03c	10.5 ± 0.0b	3.2 ± 0.5a	31.20 ± 3.24b	0.32 ± 0.01bc	1.37 ± 0.01bc	10.8 ± 0.1b	2.2 ± 0.1ab
Tem. (°C)	**Duration of exposure (h)**	**Prepupal**					**Pupal**				
		R_0	r_m	λ	T	DT	R_0	r_m	λ	T	DT
(b)											
33	0	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0b	59.80 ± 3.63a	0.36 ± 0.00	1.43 ± 0.01	11.3 ± 0.1a	1.9 ± 0.0
	2	31.90 ± 4.99b	0.32 ± 0.01b	1.37 ± 0.02b	10.9 ± 0.1b	2.3 ± 0.1a	38.55 ± 4.40b	0.33 ± 0.01	1.39 ± 0.01	10.9 ± 0.1b	2.2 ± 0.1
	4	31.65 ± 4.82b	0.33 ± 0.01ab	1.39 ± 0.01ab	10.9 ± 0.1b	2.1 ± 0.1ab	47.60 ± 3.84ab	0.35 ± 0.01	1.42 ± 0.01	11.1 ± 0.1ab	2.0 ± 0.0
	6	44.15 ± 4.61ab	0.35 ± 0.01ab	1.42 ± 0.01ab	11.0 ± 0.1ab	2.0 ± 0.1ab	42.10 ± 4.81b	0.33 ± 0.01	1.40 ± 0.02	11.1 ± 0.1ab	2.2 ± 0.2
	8	41.35 ± 4.58b	0.34 ± 0.01ab	1.41 ± 0.01ab	11.0 ± 0.1b	2.0 ± 0.0ab	43.30 ± 3.84b	0.35 ± 0.01	1.41 ± 0.01	10.9 ± 0.1b	2.0 ± 0.1
36	0	59.80 ± 3.63a	0.36 ± 0.00	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0	59.80 ± 3.63a	0.36 ± 0.00ab	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0
	2	53.05 ± 3.54a	0.35 ± 0.01	1.42 ± 0.01ab	11.1 ± 0.1ab	2.0 ± 0.1	40.15 ± 5.32b	0.33 ± 0.01ab	1.39 ± 0.01ab	11.3 ± 0.1a	2.1 ± 0.1
	4	36.95 ± 5.04b	0.32 ± 0.02	1.38 ± 0.02b	10.9 ± 0.1b	2.6 ± 0.5	43.45 ± 3.71ab	0.34 ± 0.01ab	1.40 ± 0.01ab	11.0 ± 0.1ab	2.1 ± 0.0
	6	46.80 ± 3.49ab	0.34 ± 0.01	1.41 ± 0.01ab	11.0 ± 0.1b	2.0 ± 0.0	38.25 ± 4.51b	0.32 ± 0.01b	1.38 ± 0.02b	11.0 ± 0.1ab	2.3 ± 0.2
	8	35.75 ± 4.24b	0.32 ± 0.02	1.38 ± 0.02b	10.9 ± 0.1b	2.4 ± 0.3	41.25 ± 3.95b	0.33 ± 0.01ab	1.39 ± 0.01ab	10.9 ± 0.1b	2.1 ± 0.1
39	0	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0b	59.80 ± 3.63a	0.36 ± 0.00a	1.43 ± 0.01a	11.3 ± 0.1a	1.9 ± 0.0c
	2	33.10 ± 3.81b	0.33 ± 0.01ab	1.39 ± 0.01ab	10.7 ± 0.1bc	2.1 ± 0.0b	33.65 ± 2.56b	0.33 ± 0.00a	1.39 ± 0.01a	10.7 ± 0.1b	2.1 ± 0.0bc
	4	27.65 ± 3.90bc	0.31 ± 0.01b	1.36 ± 0.01b	10.9 ± 0.1b	2.3 ± 0.1ab	27.35 ± 4.20bc	0.32 ± 0.01a	1.38 ± 0.02a	10.7 ± 0.1b	2.3 ± 0.2abc
	6	26.10 ± 2.56bc	0.30 ± 0.01bc	1.35 ± 0.01bc	10.6 ± 0.0bc	2.3 ± 0.1ab	17.30 ± 2.75c	0.27 ± 0.01b	1.31 ± 0.02b	10.7 ± 0.1b	2.7 ± 0.1ab
	8	16.70 ± 2.29c	0.27 ± 0.02d	1.31 ± 0.02c	10.5 ± 0.0c	3.0 ± 0.5a	14.90 ± 2.77c	0.25 ± 0.02b	1.29 ± 0.03b	10.6 ± 0.1b	2.9 ± 0.3a

[1] Parasitoids without exposure to heat stress treatment (control).
[2] Means followed by the same lower case letter in different durations of exposure at same temperature are not significantly different ($P < 0.05$, Tukey's HSD test).
[3] No multiple comparison, since no statistically significant differences between data sets of different durations of exposure at same temperature ($P > 0.05$).

reproductive structures might get directly damaged. Mironidis & Savopoulou-Soultani (2010) reported that heat shock can cause injury to oocytes and ovarian development; heat treated female *T. brassicae* had abnormally formed ovaries, or ovaries arrested in their juvenile state (Chihrane & Laugé, 1997).

Life-table parameters of *T. bactrae* were also affected by heat stress in our study. When exposed to 39°C during each preimaginal developmental stage, R_0, r_m, λ, and *T* were significantly decreased compared to control values. Doubling time (*DT*) is an important parameter that provides an indication of population growth. When exposed to 39°C during each preimaginal developmental stage of *T. bactrae*, *DT* was significantly increased compared to control values.

Trichogramma are more often used in biological control programs than any other natural enemy (Stinner, 1977). Adult *Tricogramma* have short life spans in the field and their parasitism success depends on their ability to cope under severe environmental conditions including heat stress (Naranjo, 1993; Ramesh & Baskaran, 1996; Maisonhaute *et al.*, 1999). Our data indicate that even small variations in temperature can potentially influence quality and efficacy of *T. bactrae* as IPM agents. Therefore, this parasitoid may be more effectively controlling lepidopterous pests during cooler weather conditions. Furthermore, in order to maintain high parasitoid activity under hot conditions, it is necessary to increase release numbers. However, the cost of heat stress has only been assessed for a limited number of traits and under laboratory conditions. In our study, only developmental aspects (emergence and deformity rate of parasitoids) and reproduction aspects (longevity and fecundity of females, life-table parameters of parasitoids) were examined. Unfortunately, other fitness components such as host localization and mating success were neglected. These important aspects might also be influenced by heat stress. In *Trichogramma* field fitness will rely on the ability of parasitoids to mate and find host eggs as well as on parasitism rate and longevity. These components still need to be tested under field condition.

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