Effects of Temperature on the Life Table Parameters of Trichogramma zahiri (Hymenoptera: Trichogrammatidae), an Egg Parasitoid of Dicladispa armigera (Chrysomelidae: Coleoptera)

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Effects of Temperature on the Life Table Parameters of *Trichogramma zahiri* (Hymenoptera: Trichogrammatidae), an Egg Parasitoid of *Dicladispa armigera* (Chrysomelidae: Coleoptera)

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ABSTRACT The influence of different temperatures on biological parameters of native strains of *Trichogramma zahiri* Polaszek (Hymenoptera: Trichogrammatidae), an egg parasitoid of rice hispa, *Dicladispa armigera* (Olivier) (Chrysomelidae: Coleoptera), was evaluated in the laboratory on its host. The key biological parameters of the parasitoid *T. zahiri* in relation to temperature were investigated to find out its candidature as a potential biological control agent of rice hispa. The highest number of eggs parasitized by *T. zahiri* was 15.7 eggs per female at 26°C, which differed significantly from those at 18, 22, 30, and 34°C ($P < 0.05$). Development duration and longevity of *T. zahiri* decreased as temperature increased. Fecundity differed significantly at all constant temperatures. Emergence rates decreased at both high (34°C) and low (< 26°C) temperatures. Female-biased sex ratio ranged from 54 to 70% at all constant temperatures. The lower temperature threshold for *T. zahiri* was 6.2°C for males and 6.95°C for females. The upper threshold temperatures were 35.82 and 35.87°C for males and females, respectively. Net reproductive rate (R_0) was highest at 26°C compared with other temperatures. Mean cohort generation time (t_G) and population doubling time (t_D) decreased as temperature increased from 18 to 30°C. The daily intrinsic rate of increase (r_m) and finite rate of increase (λ) were positively correlated with temperatures ranging from 18 to 30°C and then decreased at 34°C. The relevance of our results is discussed in the context of climatic adaptation and biological control.

KEY WORDS parasitoid, *Trichogramma zahiri*, temperature, effect, life table

Introduction

The rice hispa, *Dicladispa armigera* (Olivier) (Chrysomelidae: Coleoptera), is a serious pest causing a threat to rice production in Bangladesh. The most severe rice hispa outbreaks occurred in 1981, 1984, 1985, and 1996 when more than 0.45, 0.36, and 0.71 million ha (Khan 1989) and 0.15 million ha (Islam 1997) were affected, respectively. Outbreaks also occurred during 1987 and 1998 (Islam et al. 2009). Of the 64 districts in the country, 13 districts were affected in 1987 and 21 in 1998. Use of insecticides has been the major pest control method for the pest. However, chemical controls are now rapidly ineffective to the insect due to its resurgence and insecticide resistance arising from heavy and repeated use (Islam et al. 2009). Therefore, alternative techniques such as biological control are required to regulate *D. armigera*. Although potential natural enemies of *D. armigera* exist in rice fields of Bangladesh, little research has been done on biology of the natural enemies. So far, 183 parasitoid species have been recorded from the rice fields of Bangladesh in different seasons (Islam et al. 2003).

A trichogrammatid egg parasitoid *Trichogramma zahiri* Polaszek, an egg and larval parasitoid *Neochrysocharis* sp. (Eulophidae), and a larval and pupal parasitoid *Scutibracon hispae* (Braconidae) are active in Bangladesh. Among them, *T. zahiri* is a newly identified egg parasitoid of rice hispa reported by Polaszek et al. (2002). Body length of the parasitoid is less than 1 mm. Color is unremarkable, largely brown, with the legs, scutellum, and posterior mesoscutum pale, and the antennal flagellum is noticeably darker than the pale scape and pedicel, particularly in the female. In case of male, flagellum of antenna is three segmented, relatively short, and slightly less than 2 × length of scape. Although it can be indigenous biological control agent to suppress *D. armigera* in the rice fields of Bangladesh, detailed information is not available for its use. The rate of egg parasitism varied between zero to > 50%, with an average of 22.5% by the retrieval method and 21.8% by the field-collected method, and the highest parasitism was recorded as 53.1% (Polaszek et al. 2002). However, a recent study indicated that the parasitoid *T. zahiri* could parasitize rice hispa eggs up to 68% (Bari et al. 2005), but its role in rice hispa population

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regulation and its biology—factors that influence its success—are far from clear.

Success in biological control by *Trichogramma* depends on identification of the best host species as well as a good understanding of the ecological requirements of the parasitoid wasp (Parra et al. 1987, van Lenteren et al. 1997). However, demographic traits such as the intrinsic rate of natural increase or net reproductive rate have been estimated only in a few studies (Moghanlou 2002, Haghani and Fathipour 2004).

In insect parasitoids like *Trichogramma*, host acceptance depends not only on the host and parasitoid species but also on the abiotic environment including temperature, humidity, and photoperiod (Reznik 1995). Weather plays an important role in tritrophic interactions among poikilotherms, as it influences the level of control that natural enemies exert. Lack of success in biological control programs has often been caused by high mortality of natural enemies due to climatic extremes (Kaleybi et al. 2005).

Fertility life table is an appropriate method to study the dynamics of animal populations especially arthropods as an intermediate process for estimating parameters related to the population growth potential (Maia et al. 2000). Fertility life table is used to evaluate biological performance and to compare development of insects, such as lineage and species of *Trichogramma* (Pratissolii et al. 2004a).

One purpose of this work was to collect native *Trichogramma* wasps from rice field. In this study, we examined the quality of *T. zahiri* populations, which were produced on its host, the eggs of *D. armigera*. Therefore, the aim of this study was to estimate the developmental time, the thermal requirements and evaluate temperature effects on parasitism, sex ratio, and emergence rate of *T. zahiri*. In addition to fertility parameters, life tables were evaluated to examine the quality of *T. zahiri* produced on the eggs of *D. armigera*.

Materials and Methods

The Experimental Rice Hispa. The adult rice hispa females were allowed to lay eggs on potted BR3 rice plants in the net house of Bangladesh Rice Research Institute (BRRI), Gazipur. The plants with the females were captivated in a cage made of iron wire mesh net (1.8 by 0.6 m). The plants were then transferred to a water-filled galvanized tray (2.13 by 0.93 m) after 3 d of oviposition for grub development. During the pupal stage, the plants were transferred to another wire mesh cage for collection of the adults. The newly emerged adults were transferred to another cage with 30-d-old healthy rice plants, and the adults were allowed to mate for a week. Finally, the mated pairs were shifted to an egg-laying cage for oviposition in the net house.

Collection and Rearing of *T. zahiri*. Population of *T. zahiri* were collected from eggs of the rice hispa by retrieval methods at BRRI farm. Potted rice plants with freshly laid rice hispa eggs were placed in the rice field so eggs could be parasitized by *T. zahiri*. Two days after placement, rice leaves with rice hispa eggs were collected and reared in test tubes (23 by 8 cm^2). A few drops of water was placed at the bottom of the test tubes and tightly closed by cotton lids wrapped with a fine-mesh nylon net. Test tubes were checked regularly for emerged parasitoids, which were separated in another test tube and used in different tests. Based on morphometric analysis by Polaszek et al. (2002), wasps were identified as *T. zahiri*. Antennal characters were used to separate female and male *Trichogramma* individuals. Fresh rice hispa eggs were exposed to freshly emerged *T. zahiri* in the test tubes regularly for its multiplication. The *T. zahiri* was reared on eggs of the host routinely in the parasitoid rearing laboratory at around 25°C, 65% relative humidity (RH), and a photoperiod of 16:8 (L:D) h.

Fecundity and Development of *T. zahiri* at Different Temperatures. One or two leaf pieces containing a total of 15–20 rice hispa eggs were kept in a test tube (23 by 8 cm^2), and the lower end of the leaf pieces was wrapped with water-soaked cotton wool to maintain leaf turgidity. Freshly emerged single mated females of *T. zahiri* were introduced into each test tube for egg laying on rice hispa eggs and replaced by new sets of eggs every day until the death of female. Fresh host eggs were provided daily; the number of eggs offered was more than the maximum daily egg-laying capacity of the female. Honey was provided as food in the test tube. This was done for three cohorts of 10 individuals for each of the five temperatures (i.e., 18, 22, 26, 30, and 34°C). Therefore, every trial had 30 replications, and the experiment was conducted by completely randomized block design. The number of offspring produced per female was determined at five constant temperatures and 65 ± 5% RH in the incubator. The number of sex of the progeny was recorded daily. Parasitism was determined by counting host eggs turned black owing to parasitism. After hatching of the progeny, all the parasitized host eggs were dissected under microscope to confirm parasitism by *T. zahiri*.

The development duration was determined by allowing the host eggs parasitized to develop into adult. Five days after deposition of parasitizing eggs, leaves were cut into small pieces, and each contained a single parasitized rice hispa egg, which was placed into a 5-ml glass vial with a few drops of water.

These vials were then placed in the incubator at the above-mentioned five constant temperatures separately and checked daily for emergence of progeny. The development duration from egg to adult was determined by five cohorts of 20 male and female of *T. zahiri* emergence recorded from a constant temperature. Thus, every trial had 100 replications.

Thermal Threshold and Thermal Constant. Ikemoto and Takai's (2000) model was used to estimate the thermal threshold and constant. The law of total effective temperature applied to the temperature-dependent development of arthropods was expressed by the equation: $DT = k + tD$, where D is the duration (d) of development, T is environmental (mean or isothermal) temperature (°C), t is lower threshold temperature, and k represents thermal constant. The equation of the nonlinear thermodynamic model is applicable (Ikemoto 2005, 2008) for a wide range of temperatures.

Life Table Parameters. Daily age-specific survival (l_x) and fecundity (m_x) rates were used to generate life tables of *T. zahiri* for each temperature.

The intrinsic rate of natural increase (r_m) was estimated from the life-time fecundity table according to the equation:

$[\sum e^{-r}\ \mathrm{m}^{x}\ l_x m_x = 1]$, given by Birch (1948),

where x is female age in days, l_x is the age-specific survival rate, and

m_x is the expected number of daughters produced per female alive at age x (Sabelis 1985, Gotoh and Gomi 2003, Gotoh et al. 2010, Ullah et al. 2010).

The net reproductive rate (R_0) is given by $[R_0 = \sum l_x m_x]$,

The mean generation time (t_G) in days is given by $[t_G = ln\ R_0/r_m]$,

The finite rate of increase (λ) is given by $[\lambda = e^{rm}]$, and

The doubling time (t_D) in days is $[t_D = ln\ (2)/r_m]$.

After r_m was computed from the original data (r_{all}), the standard errors for the life history parameters at different constant temperatures were estimated using the Jackknife method (Meyer et al. 1986, Maia et al. 2000).

Briefly one of the parasitoid is omitted and r_m (r_i) is calculated for the remaining parasitoids ($n-1$). Based on Meyer et al. (1986), the Jackknife pseudovalue (r_j) is computed for this subset of the original data according to the equation $[r_j = n\ r_{\mathrm{all}} - (n-1)r_{i]}$.

This process was repeated for all possible omissions of one parasitoid from the original dataset to produce pseudovalues, which allowed for computing confidence limits for the parameter values (Ullah et al. 2011).

Statistical Analysis. Data were analyzed by means of analyses of variance, using temperature as an explanatory variable. The purpose was to quantify relationships between the response variables (eggs per female, hatch rate, survival rate, sex ratio, adult longevity, development duration from egg to adult, net reproductive rate, and intrinsic rate of increase) and predictor variables [gender (G) and temperature (T)] with a view to find out which of the predictors contribute most to explain the variation in data.

The data of response variables were subjected to a logarithmic transformation prior to analysis with a view to stabilize the variance and also confirm that the back-transformed values were nonnegative.

To estimate the predicted, lower and upper level values (95% CI) of a response variable, we used linear model in regression procedure where temperature (T) and temperature square (T^2) were used as predictor variables to fit the data. The variables parasitization rates, developmental times, parasitoid's emergence, and sex ratio between treatments were compared using a one-way analysis of variance followed by Tukey's post hoc test at 0.05 level.

Results

Effect of Temperature on Parasitization and Offspring Production of *T. zahiri*. Parasitization, fecundity, offspring production, and sex ratio of *T. zahiri* were influenced by temperature (Table 1). The average number of eggs parasitized by *T. zahiri* was 15.67 eggs per female at 26°C, which differed significantly from those at 18, 22, 30, and 34°C ($P < 0.05$). The lowest parasitism was 6.13 and 5.33 eggs per female at low (18°C) and high (34°C) temperature, respectively (Table 1). The fecundity of *T. zahiri* was strongly influenced by temperature and showed significant differences among treatments. Total offspring production per female varied significantly with temperature, and the highest was 31.93 at 26°C, which was different from the effects of 18, 22, 30 and 34°C. Significantly fewer eggs and offspring production per female was observed at both low (18°C) and high (34°C) temperatures. There was no significant difference in offspring production per female at temperature 22 and 30°C (Table 1). Offspring sex ratio of *T. zahiri* varied with temperature, showing a female-biased population at all temperature regimes. The sex distribution of the parasitoid at 26°C showed the highest proportion of female individuals, which differed significantly with 18 and 34°C. The effects of temperature on the sex ratio and offspring production per parasitized eggs were highly significant ($P < 0.05$). Successful offspring production in each parasitized egg increased with temperature up to 26°C, and then declined as temperature increased to 34°C. However, no significant differences were detected within temperature between 22 and 30°C (Figs. 1–3).

Table 1. Parasitization, fecundity, offspring production, proportion of female sex, and development duration of *T. zahiri* at different temperatures

Temp (°C)	Pasitized egg (no.) (Mean ± SE)	Egg laid per female (Mean ± SE)	Offspring production (Mean ± SE)	Female sex ratio (Mean ± SE)	Dev. duration d (Mean ± SE) Male	Dev. duration d (Mean ± SE) Female	Offspring per egg (Mean ± SE)
18	6.13 ± 0.23c	18.53 ± 0.98c	8.53 ± 0.58c	0.58 ± 0.01	15.03 ± 0.44a	15.19 ± 0.05a	1.37 ± 0.05b
22	11.73 ± 0.32b	30.27 ± 0.96b	21.6 ± 0.76b	0.68 ± 0.02	12.04 ± 0.46b	12.22 ± 0.05b	1.84 ± 0.06a
26	15.67 ± 0.45a	37.47 ± 1.43a	31.93 ± 1.33a	0.70 ± 0.05	10.13 ± 0.54c	10.42 ± 0.04c	2.01 ± 0.07a
30	12.27 ± 0.49b	28.80 ± 1.27b	23.20 ± 1.06b	0.66 ± 0.03	7.44 ± 0.33d	7.49 ± 0.04d	1.90 ± 0.05a
34	5.33 ± 0.20d	12.87 ± 0.42d	6.73 ± 0.27c	0.54 ± 0.02	7.01 ± 0.43e	7.36 ± 0.04e	1.28 ± 0.04b
F-value	*69.24	*64.52	*64.52	$\chi^2 = 69.60$, df = 4, $P < 0.05$	*378.90	*290.86	*23.82

Means within a column followed by the same letter are not significantly different ($P < 0.05$; Tukey's post hoc test).

*Significant at 5% level.

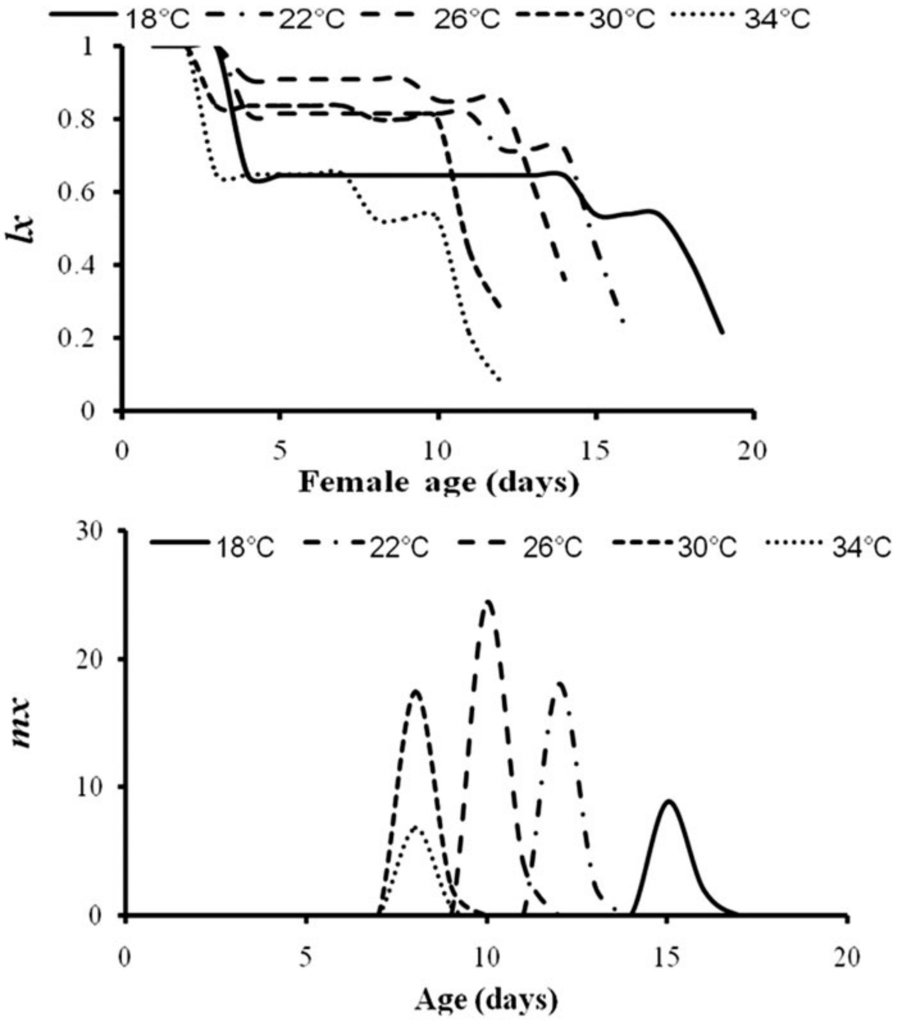

Fig. 1. Temperature effects on oviposition rate (eggs per female). Points show the sample averages with 95% CI. The heavy lines show the predictions based on the generalized linear models. Thin lines represent the 95% CI (upper and lower) for the predicted line. Error bars represent standard errors.

Egg-to-Adult Development Duration in *T. zahiri*. Development (egg to adult) duration in the parasitoid *T. zahiri* varied significantly at different constant temperatures. The mean development duration for male and female ranged from 7.0 to 15.0 d and 7.4 to 15.2 d, respectively (Table 1). The development duration for both male and female was longest at 18°C and shortest at 34°C. Unlike other trichogrammatid egg parasitoids, female *T. zahiri* did not take significantly longer time then males to reach adulthood. The Tukey's post hoc test did not show significant variation in the development duration of male and females at a particular temperature ($P < 0.05$; Table 1 and Fig. 4).

At 34°C, *T. zahiri* developed faster than that at 18, 22, 26 and 30°C. Generalized linear model showed development duration for males increased from 7.0 d to 15.0 d when temperature decreased from 34 to 18°C. Similar trend was also appeared in female development duration (Table 1 and Fig. 4)

Ikemoto and Takai's linear model, when fitted to values of developmental rates, gave a close fit to the data at temperature ranging from 18 to 34°C ($0.942 \le r^2 \le 0.945$; Table 2 and Fig. 5). The estimated lower thresholds ($t = T_L$) for egg to female adult and egg to male adult development were very similar, and were 6.21 and 6.95 respectively (Table 2). Ikemoto's nonlinear model, when fitted to values of developmental rates, gave a close fit to the data at temperatures ranging from 18 to 34°C ($0.0008 \le \chi^2 \le 0.0010$; Table 2 and Fig. 5). The intrinsic optimum temperature (T_Φ) for egg to female adult and egg to male adult were 24.4 and 24.8°C, respectively (Table2).

The upper developmental thresholds (T_H) were also very close, and were 35.87 and 35.82°C for egg to female and egg to male adult, respectively (Table 2).

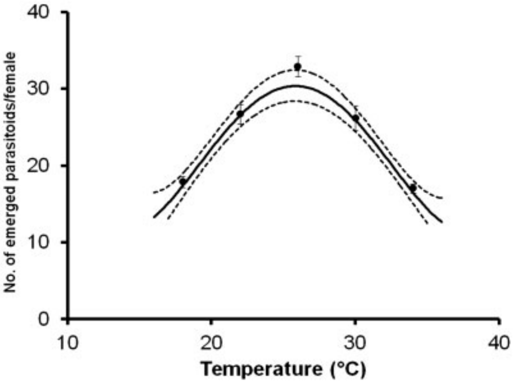

Fig. 2. Temperature effects on sex ratio expressed as proportion of female *T. zahiri* adults that are females. Points show the sample averages with 95% CI. The heavy lines show the predictions based on the generalized linear models. Thin lines represent the 95% CI. (upper and lower) for the predicted line. Error bars show standard errors.

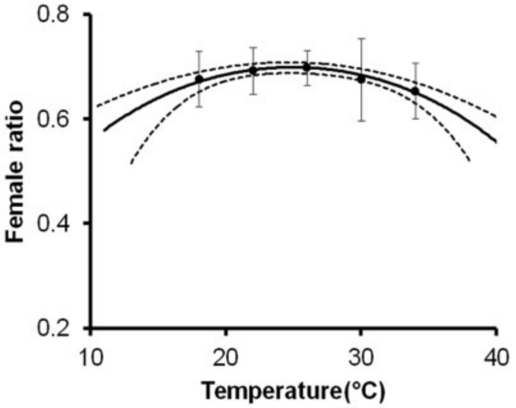

Fig. 3. Temperature effects on number of parasitoids emerged from each female *T. zahiri*. Points show the sample averages with 95% CI. The heavy lines show the predictions based on the generalized linear models. Thin lines show the 95% CI (upper and lower) for the predicted line. Error bars show standard errors.

Life Table Parameters of *T. zahiri*. Age-specific survival (l_x) and fecundity rate (m_x) of *T. zahiri* were determined through studying the number of eggs laid, their hatchability, survival rate, and the proportion of female offspring. The age-specific survival rate (l_x) started to drop at earlier ages as temperature increased from 18 to 34°C (Fig. 6). The age-specific fecundity rate (m_x) showed its peak at 26°C, and then decreased as temperature increased to 34°C. Fecundity of the parasitoid remained low at lower temperatures of 18 and 22°C (Fig. 6).

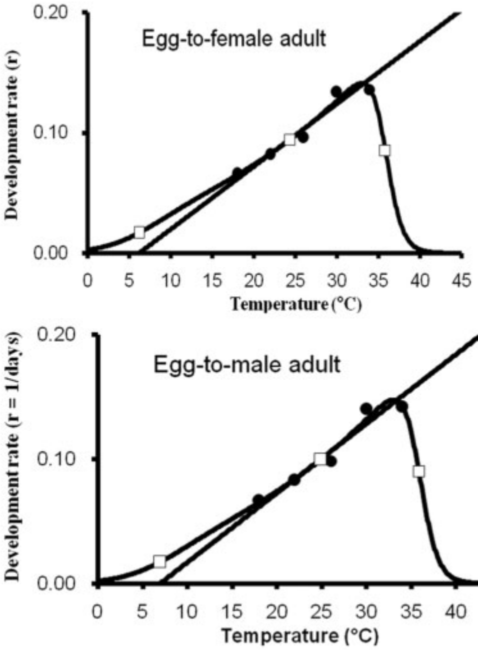

Fig. 4. Temperature effects on the developmental time for egg-to-male adult and egg-to-female adult in *T. zahiri*. Points show the average values observed. The heavy lines show the predictions based on the generalized linear models. Dotted lines show the 95% CI (upper and lower) for the predicted line. Error bars show standard errors.

The net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), and the mean generation time (t_G) were affected by temperature, and there were significant differences among temperature responses (Table 3 and Fig. 7). The net reproductive rate significantly differed with variable temperature ($F = 2.635$, df = 4, $P < 0.05$). The highest (R_0) value was 24.34 observed at 26°C, whereas the lowest value was 3.95 found at 34°C. The intrinsic rate of increase (r_m) of *T. zahiri* was found to be significantly different ($F = 970.484$, df = 4, $P < 0.05$), among rearing temperatures. The r_m values increased with increasing temperature from 18 to 34°C but peaked at 30°C (0.34 d^{-1}). Mean generation time (t_G) decreased significantly with increasing temperature, ranging from 15.2 d at 18°C to 8.2 d at 34°C. The maximum value for the mean generation time was observed as 15.2 d at 18°C. Doubling time (t_D) differed significantly and was found to decrease with increasing temperatures, and varied from 6 d at 18°C to 2 d at 30°C ($F = 789.163$, df = 4, $P < 0.05$; Table 3). A sudden increase of t_D to 4.2 d at 34°C was noticed.

The cohorts reared at 18°C had the highest t_D value of 6.05 d, indicating that a population of the parasitoid would double during this period of time. This parameter had significant differences among temperatures from 18 to 34°C. In addition, the finite rate of increase was significantly affected ($F = 921.482$, df = 4, $P < 0.05$) by temperature. The values increased with increasing temperature from 18 to 34°C but reached a peak at 30°C (1.41 d^{-1}), and the lowest value was 1.12 d^{-1} at 18°C (Table 3).

Table 2. Estimated values of constants in linear and nonlinear models describing the relationship between temperature (°C) and developmental rates of *T. zahiri*

Stage	Law of total effective temperature linear model			
	t (± SE)	k (± SE)	r^2	Linear model equation
Egg-to-female adult	6.207 ± 2.21	192.221 ± 24.26	0.945	Y = 0.0052 × – 0.0323
Egg-to-male adult	6.950 ± 2.15	179.114 ± 23.14	0.942	Y = 0.0056 × – 0.0388

Thermodynamic nonlinear model (SSI model)

	$[T_\Phi](k)$	T_Φ(°C)	ρ	ΔH_A (cal/deg.mol)	ΔH_L (cal/deg.mol)	ΔH_H	$[T_L]$	$[T_H]$(°C)	χ^2
Egg-to-female adult	297.55	24.4	0.0946	8810	−49040	19687	279.36	35.87	0.00084
Egg-to-male adult	298.05	24.8	0.0997	9293	−49215	19444	280.10	35.82	0.00101

t, lower threshold temperature (°C); k, thermal constant (°C); T_Φ, intrinsic optimum temperature (°C); ρ, developmental rate at T_Φ; ΔH_A, enthalpy of activation; ΔH_L and ΔH_H, change in enthalpy associated with low and high temperature inactivation of enzyme, respectively; T_L, temperature at which enzyme is half active; T_H, upper threshold temperature.

The potentiality of the parasitoid *T. zahiri* was evaluated as a biocontrol agent of *D. armigera* through studying a number of its biological parameters. Temperature was found to play an important role in the egg laying, emergence rate, female ratio, and development of *T. zahiri*. The egg laying of *T. zahiri* was influenced by temperature and showed increasing trend up to 26°C and then decreased again (Fig. 1). Female ratio and emergence of *T. zahiri* were higher at 26°C temperature (Figs. 2 and 3). Development duration decreased with the increase of temperature irrespective of sex (Fig. 4). The rate of development of *T. zahiri* was accelerated as temperature increased (Fig. 5). In the life table study of *T. zahiri*, it was found that the net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), and the mean generation time (t_G) were affected by the temperature, and there were significant differences among with variable temperatures. The highest (R_0) value was found at 26°C whereas lowest at 34°C. Intrinsic rate of increase (r_m) of *T. zahiri* was accelerated with increasing temperature and reached a peak at 34°C. Mean generation time (t_G) decreased significantly with increasing temperature (Fig. 7).

Discussion

Effect of Temperature on Parasitization and Offspring Production in *T. zahiri*. Temperature significantly influenced parasitism, fecundity, parasite emergence, and sex ratio of the parasitoid *T. zahiri*. The parasitism of *T. zahiri* accelerated significantly as temperature increased from low (18°C) to moderate (26°C), and then declined to a minimum at high temperature (34°C). A two- to threefold higher egg laying was observed at a moderate temperature of 26°C. This indicates that to build up population of *T. zahiri* rapidly, an optimum temperature is a prerequisite. In the present study, a great variation in the fecundity of the parasitoid at different temperature regimes was observed, which should be taken into consideration for using it in the biocontrol program. Highest number of eggs laid by a rice hispa was 17.55 eggs per day per female, of which 31 to 81% eggs were parasitized by the parasitoid in different seasons (Bari 2013).

Being a pro-ovigenic parasitoid, *T. zahiri* adult began oviposition from the first day of eclosion. In most cases, egg laying completed within 2 d of emergence. Omer et al. (1996) and Choudhury (2002) also found a similar oviposition pattern in the leaf miner parasitoid, *Ganaspidium utilis* Beardsley, and glasshouse leafhopper egg parasitoid, *Anagrus atomus* (L.), respectively. They showed highest progeny production in day 2 and day 3 of the parasitoid's reproductive life. Average fecundity of *T. zahiri* was found to be highest at 26°C and then decreased as temperature increased. The decreased fecundity at high temperatures may be due to the reduction in longevity of the female parasitoids. Baitha and Ram (1998) reported a decreased fecundity and longevity of the egg parasitoid *Trichogrammatoidea armigera* Nagaraja with increasing rearing temperature. Choudhury (2002) found lower maturation rate and less egg production in *A. atomus* at 25°C than those reared at 17°C. van Huis et al. (1994) found a significant effect of temperature on population increase in the trichogrammatid *Uscana lariophaga* Steffan.

The highest emergence of *T. zahiri* was recorded at 26°C, which was significantly different from other treatments. Emergence was found to be reduced drastically at low (18°C) and high (34°C) temperatures. This indicates that population build-up at 18°C or lower and 34°C or higher would be difficult. Pavlik (1990) studied the effect of three different temperatures on five *Trichogramma* species and observed significant differences in parasitism. Several authors have shown that among physical factors, temperature exerts the strongest influence on the biological characteristics of *Trichogramma* spp. (Park et al. 2000, Pratissoli and Parra 2000a, Haile et al. 2002, Botto et al. 2004, Ozder and Kara 2010). The present results are the consistent with that of the above studies.

Park et al. (2000) found emergence rate of *Trichogramma dendrolimi* Matsumura tended to be lower at 30–32°C and higher at 26–28°C. Lower offspring production was also found at lower temperatures between 18 to 22°C. This could be related to lower

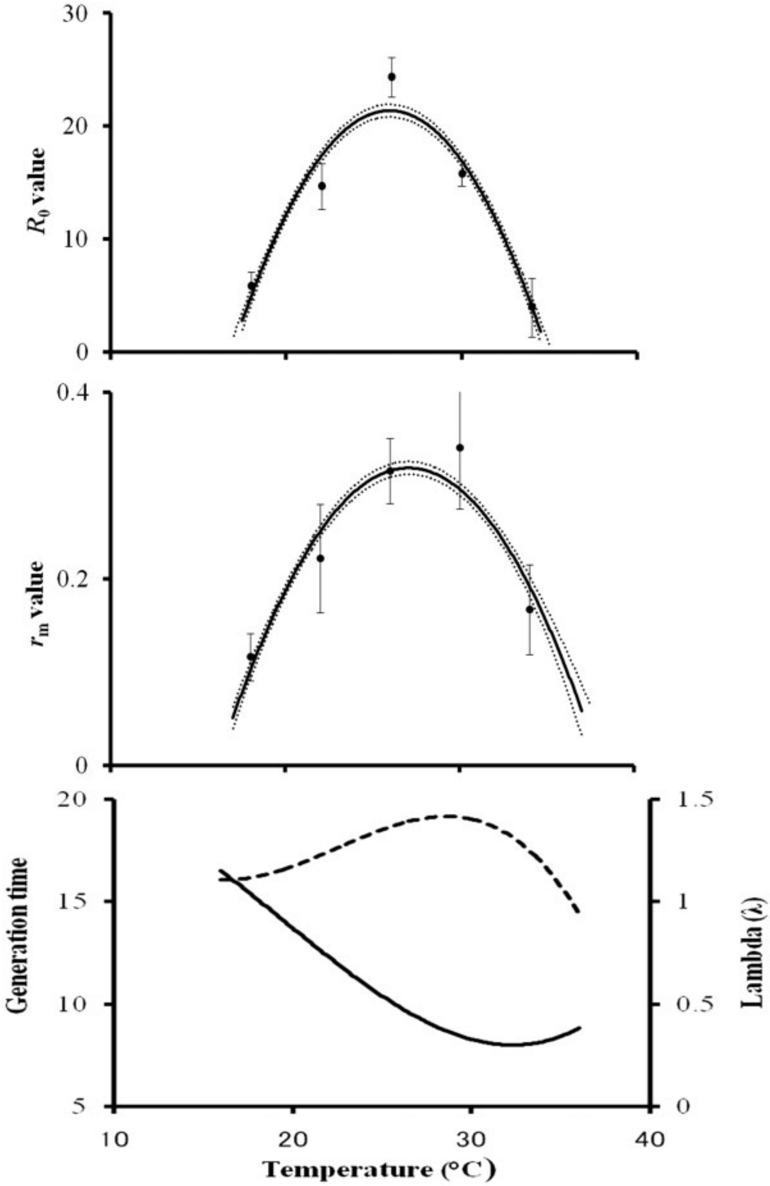

Fig. 5. Linear and thermodynamic (nonlinear) models fitted to the temperature-dependent development of *T. zahiri* (Ikemoto and Takai's 2000). Circles show data points. Squares in order (from left to right) represent lower (t), middle (T_φ), and upper (T_H) constant values estimated by nonlinear model.

metabolic process with very little biological activities at lower temperature regime. Although a number of authors reported that slight variations of temperature could cause significant changes in emergence of many *Trichogramma* spp including *T. zahiri*, Harrison et al. (1985) showed different results when *Trichogramma exiguum* and *Trichogramma pretiosum* were reared on *Heliothis vireguum* (F.) eggs. They found no significant differences in emergence rate within temperatures except at 25 and 35°C. However, it should not be expected that all the *Trichogramma* species would react with the temperature to the same extent. Individual difference in different species is common in nature.

Regardless of temperature, there were more females than males in *T. zahiri*. Harrison et al. (1985) reported temperature affected the sex ratio of *T. exiguum* and *T. pretiosum*, with females slightly less abundant at lower and upper developmental temperatures. The present results also showed that temperature could affect the sex ratio. Female percentage ranged from 54 to 70, which is consistent with Haile et al. (2002), who found that sex ratio was biased to female production at all temperatures.

Egg-to-Adult Development Duration in *T. zahiri*. The development duration for both male and female *T. zahiri* varied significantly at different

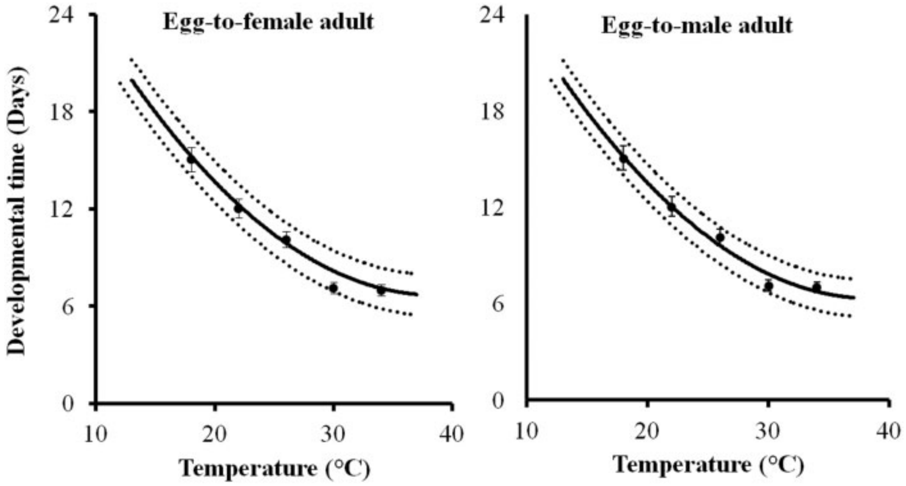

Fig. 6. Age-specific survival rate (l_x, upper panel) and age-specific fecundity rate (m_x, bottom panel) of females of *T. zahiri* at different temperatures.

Table 3. Life table parameters (mean ± SE) of *T. zahiri* at different temperatures under a photoperiod of 16:8 (L:D) h: intrinsic rate of natural increase (r_m, d^{-1}), net reproductive rate (R_0), mean generation time (t_G, d), finite rate of increase (λ), doubling time (t_D, d)

Tempreture (°C)	N	r_m	R_0	t_G	λ	t_D
18	30	0.116 ± 0.004e	5.83 ± 0.008d	15.19 ± 0.340a	1.12 ± 0.003e	6.05 ± 0.129a
22	30	0. 222 ± 0.004c	14.64 ± 0.017c	12.16 ± 0.150b	1.25 ± 0.0.003c	3.14 ± 0.037c
26	26	0.316 ± 0.003b	24.34 ± 0.025a	10.13 ± 0.083c	1.37 ± 0.003b	2.20 ± 0.017d
30	20	0.341 ± 0.006a	15.78 ± 0.036b	8.13 ± 0.127d	1.41 ± 0.007a	2.04 ± 0.030e
34	20	0.167 ± 0.003d	3.95 ± 0.005e	8.24 ± 0.147d	1.18 ± 0.003d	4.16 ± 0.070b
Level of significance		*F*-value = 970.484, $P < 0.05$	*F*-value = 2.64, $P < 0.05$	*F*-value = 262.42, $P < 0.05$	*F*-value = 921.48, $P < 0.05$	*F*-value = 789.16, $P < 0.05$

Means within a column followed by the same letter are not significantly different ($P < 0.05$; Tukey's post hoc test). N, number of females tested.

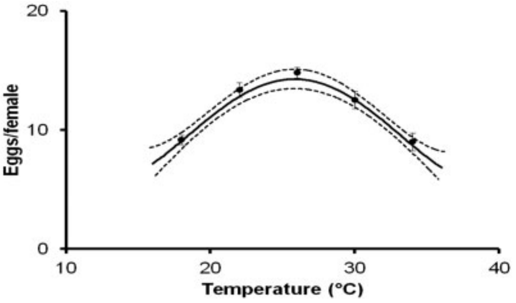

Fig. 7. Effect of temperature on demographic patterns of *T. zahiri*. R_0, net reproductive rate; r_m, intrinsic rate of natural increase; t_G, mean generation time; λ, finite rate of increase. The heavy lines for R_0 and r_m show the predictions, based on generalized linear model. Dotted line represents 95% confidence limits for the predictions. In the bottom figure, dotted line indicates λ, and straight line indicates t_G.

temperatures. In laboratory experiments with five different constant temperatures, it was found that development duration of the parasitoid, *T. zahiri* decreased with the increase of temperature irrespective of sex. The developmental duration decreased from 15.13 to 7.19 d when temperature increased from 18 to 30°C irrespective of sex. The trend of variation among temperatures was similar for both sexes. Females always had slightly longer development duration than males, but the difference was statistically insignificant. *T. zahiri* developed successfully from egg to adult at temperatures ranging from 18 to 34°C. The development of *T. zahiri* was clearly temperature dependent. Being a member of poikilothermic animal, it is normal for *T. zahiri* to show variation in development duration under variable environmental temperatures. Reports on the development duration of other *Trichogramma* species indicate that they respond readily to the change in environmental temperature (Park et al. 2000, Scholler and Hassan 2001). Increase in temperature usually leads to decrease in development duration upto certain limit. However, the decreasing trend is limited to a range of moderate temperatures. The present experimental result showed no marked change in development duration after 30°C. Park et al. (2000) reported that the rate of development of *T. dendrolimi* accelerated as temperature increased. The temperature at and above 34°C could not contribute to the development of *T. zahiri*. Although further high temperature was not evaluated for the development, temperature beyond 34°C could have deleterious effect on the development. Scholler and Hasan (2001) showed that at 35°C the parasitized host turned black for both the species

Trichogramma evanescens and *Trichogramma cacoeciae* but no progeny emerged, indicating detrimental effect of high temperature. Polaszek et al. (2002) found that the development period (egg to adult) of *T. zahiri* varied from 6 to 11 d, averaging 8.2 d. Maximum (94%) individuals completed the development at the laboratory temperature between 30.1 to 30.9°C. Therefore, in general, development duration for *Trichogramma* sp. varies greatly with temperature and to some degree between species. Most species required 12 to 13 d at 23–25°C (Pinto 1998). In the present study, development duration of *T. zahiri* was 12 d at 22°C which is similar with that study.

Development time needed by *T. zahiri* was shorter as temperature increased, which was in agreement with Consoli and Parra (1995). It is assumed that this might be due to a more appropriate metabolic process of the immature stages. In this study, temperature thresholds and thermal requirements were estimated using linear and nonlinear thermodynamic models (Fig. 5). Extrapolation of linear regression lines of developmental rate and temperature showed that the lower threshold temperatures (t) for egg to female adult and male adult are 6.21 and 6.95°C, respectively. A thermodynamic nonlinear model (Optim SSI) was used to estimate the intrinsic optimum temperature (T_Φ) for development. Based on enzyme activity, other parameters were also estimated. In this program, the results of a linearized formula (Ikemoto and Takai 2000) based on the reduced major axis method were also obtained. This Sharpe–Schoolfield–Ikemoto (SSI) model is a nonlinear thermodynamic model improved by Ikemoto (2005, 2008) and Shi et al. (2011) on the basis of the SS model developed by Sharpe and DeMichele (1977) and Schoolfield et al. (1981). In this model, the intrinsic optimum temperature (T_Φ) for development is the most important thermal parameter. Ikemoto (2005) devised a program for estimating the parameters in the SSI model. Shi et al. (2011) modified this program and developed SSI-P, which runs on R statistical software (www.rproject.org) for faster estimation of the parameters. Ikemoto et al. (2012) further improved this program, creating Optim SSI-P by incorporating the optimization algorithm of Nelder and Mead (1965), wherein T_Φ was estimated along with its confidence intervals. In this paper, Optim SSI program (version 2.7), which runs on R statistical software, was used to estimate the thermodynamic model parameters.

Intrinsic optimum temperature (T_Φ) of 26°C was obtained for the total development from egg to adult, suggesting the maximal active state enzymes involved in the developmental process. The upper (T_H) and lower (t) threshold temperatures were estimated at 35.82 to 35.87 and 6.21 to 6.95°C for total development, suggesting that the hypothetical enzyme was half active and half inactive at these thresholds. This could be one of the reasons for the incomplete development of the larval stage at this temperature. The intrinsic optimum temperature along with its confidence interval could be used as an indicator for the geographical distribution and place of origin of related species (Ikemoto 2003). This is also a potential tool for the construction of a phylogenetic tree within a taxon (Ikemoto et al. 2012).

The optimal temperature for development of *T. zahiri* was 26°C. Similar optimum temperature for *Trichogramma platneri* was reported by McDougall and Mills (1997). In the present study, total development time for *T. zahiri* was almost doubled (15.19 d) at 18°C than at 34°C (7.36 d). Four times higher variation in development duration of *T. platneri* was reported by McDougall and Mills (1997). Hansen (2000) also reported temperature-dependent development in *Trichogramma turkestanica*.

Life Table Parameters of *T. zahiri*. Temperature is one of the major abiotic factors affecting the development rate, cumulative fertility, longevity, sex ratio, and emergence rate of *Trichogramma* spp. A temperature-dependable life table of *T. zahiri* was estimated using the biological characteristics such as rate of parasitism, development, sex ratio, emergence rate, and adult longevity. Temperature was found to have influence on all parameters studied.

Life table parameters differed significantly in response to the different temperature treatments, and showed a varied net reproduction rate (R_0) of *T. zahiri* from 3.95 to 24.34 according to temperature variation. The maximum increase in net reproduction rate (24.34) was found at 26°C. Pratissoli and Parra (2000b) found that the net reproduction rate varied with temperature for *T. pretiosum*. Cabello and Vargas (1988) related the reduction of the net reproductive rate at high temperatures to the production of both males and females at these temperatures. This can explain why the R_0 in the present study was reduced at 34°C.

Pratissoli and Parra (2000a) demonstrated that not only high (>25°C) but also lower temperatures (<22°C) affected the net reproductive rate of *T. pretiosum* negatively. The net reproductive rate was affected negatively by temperatures below or above 25°C, and consequently, the population growth capacity was extremely reduced (Pratissolli et al. 2004b).

The intrinsic rates of increase (r_m) of the parasitoid *T. zahiri* for the different temperatures varied significantly, and the highest rate was found at 30°C. Cohort generation time (t_G) differed significantly at variant temperatures. The finite capacity for increase (λ) of the parasitoids increased with increasing temperature. Doubling time (t_D) decreased with the increase of temperature; the longest time required occurred at 18°C and the shortest time at 30°C. The results of these life table parameters were consistent with several other studies (Pratissoli and Parra 2000b, Scholler and Hassan 2001, Zhang et al. 2001, Haile et al. 2002, Ozder and Kara 2010, Samara et al. 2008, 2011), and indicated positive attributes for *T. zahiri* as a potential biocontrol agent of rice hispa.

Results obtained from the study of life table parameters of the parasitoid *T. zahiri* showed that temperature ranging from 26 to 30°C is favorable for its growth, development, and survival. This fit into the particular range of temperature prevailing in Bangladesh for most of the rice-growing seasons, indicating that *T. zahiri* is a well-suited species in the locality. Moreover, parasitism performance of *T. zahiri* on rice hispa eggs and successful offspring production in the laboratory condition also indicates that this species could be a promising biocontrol agent for its rearing. Growers and pest management advisors must carefully evaluate this *Trichogramma sp* to determine if and how this temperature-dependent life table can best fit into their integrated pest management (IPM) programs. This laboratory data would definitely be a base in evaluating its field performance through semifield and field experiments. Therefore, this finding is expected to provide important information in designing a comprehensive program for IPM of rice hispa in Bangladesh. However, further studies on the parameters such as searching behavior, diapauses and dispersal, and suitable alternate hosts for rearing need to be undertaken for its better use in IPM program.

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Host Egg Age and Supplementary Diet Influence the Parasitism Activity of *Trichogramma zahiri* (Hymenoptera: Trichogrammatidae)

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Abstract

Mass production of egg parasitoids mostly depends on the age of the host. Generally old eggs are less preferred by egg parasitoids, which can discriminate between eggs of different ages by using chemical cues. This study was designed to determine the preference, development, and arrestment of *Trichogramma zahiri* Polaszek (Hymenoptera: Trichogrammatidae) parasitizing eggs of its native host, the rice hispa, *Dicladispa armigera* (Olivier) (Coleoptera: Chrysomelidae). Eggs of different ages, in addition, with or without supplementary foods were evaluated. *T. zahiri* preferred to parasitize 1-d-old eggs rather than 2-, or 3-d-old eggs by no-choice assays. However, although the percentage emergence of parasitoids is significantly lower from 2- and 3-d-old eggs, the sex ratio is unaffected. Parasitoids lived longer when 25% honey solution was provided with the host food. Significantly higher fecundity (38.5 eggs per female) and parasitoid emergence (94.6%) occurred when 25% honey solution was provided in the diet with host food, followed by 25% sugar solution, as compared to the control (only water as food). An average of 7.9 eggs were parasitized when one parasitoid was released per 10 rice hispa eggs. Ability of *T. zahiri* to parasitize egg increased with an increase in the number of eggs offered. We also found that inclusion of a fresh host egg with the supplementary diet improves the mass rearing of *T. zahiri* for commercial purposes.

Key words: host age preference, *T. zahiri*, density dependent, fecundity, diet

The performance of a parasitoid depends in part on its host selection behaviors (Vinson 1976, 1984). Especially, egg parasitoids can effectively identify and select their host based on host age, usually preferring recently oviposited eggs, because old eggs adversely affect the biological activity of a parasitoid, including parasitism rate (%) and the egg–adult emergence period (Da Rocha et al. 2006, Bruce et al. 2009), body weight, and offspring sex ratio (Ruberson and Kring 1993). The freshly laid egg is more suitable than old one because nutrient quality and chemical composition of host eggs deteriorate with the development of the host embryo as well as the egg chorion, which becomes hard with age (Barret and Schmidt 1991, Bai et al. 1992). Egg parasitoids select suitable age hosts in order to increase their fitness (Pyke et al. 1977, Strand and Vinson 1983, Schmidt and Smith 1985, Vinson et al. 1998). Parasitoids identify their perfect host eggs utilizing physical and chemical indicators found in and on the surface of eggs (Borges et al. 1999, Hilker and Meiners 2002). In this way, egg parasitoids avoid older eggs (poor quality food) through host-derived chemical signals (Kennedy 1978, Beevers et al. 1981, Gazit et al. 1996).

Trichogramma is an important biocontrol agent, mainly of Lepidopteran eggs, and are used as biocontrol agents against several insect pests all over the world (Li 1994, Smith 1996). *Trichogramma* can be mass-reared in the laboratory using alternative hosts, including *Anagasta kuehniella* (Zeller), *Sitotroga cerealella* (Olivier), *Plodia interpunctella* (Hubner), *Galleria mellonella* (L.), and *Corcyra cephalonica* (Stainton) (Smith 1996, Greenberg et al. 1998, Shojai et al. 1998, Ebrahimi 2004). Mass rearing provides a large number of parasitoids within a short time that can be later released in the field as biocontrol agents against certain other insect pests. *Trichogramma* can be used in a variety of crops including sugarcane, rice, soybean, cotton, sugar beet, vegetables, and pine trees as a biocontrol agent (Hassan and Guo 1991, Pinto and Stouthamer 1994) to regulate pest populations by parasitization of the host egg stage. *Trichogramma* use in a plant protection programs span >32 million ha of agricultural crops and forest lands (Li 1994).

Trichogramma zahiri (Polaszek) is an egg parasitoid of rice hispa, *Dicladispa armigera* (Olivier) (Coleoptera: Chrysomelidae), which is a serious pest of rice in Bangladesh, and other south Asian countries (Polaszek et al. 2002). Rice hispa has a long history of sporadic outbreaks in Bangladesh, where yield losses have been determined to be as high as 40–50%, and have increased in recent years (Bari et al. 2015). Currently, the pest management practice of the rice hispa solely depends on chemical insecticides, hence the need to develop alternative management technologies. *T. zahiri* is an indigenous parasitoid of *D. armigera* in Bangladesh, so, may be developed for large-scale commercialization, to use this parasitoid as an augmentative biocontrol agent. Polaszek et al. (2002) reported 53% parasitism, whereas *T. zahiri* can parasitize up to 68% of rice hispa eggs in the field as reported by Bari et al. (2005). At other times, *T. zahiri* shows up to 86% parasitism of rice hispa eggs during the Transplanted Aman phase of the rice production season (Bari 2013). Other studies showed that the life table parameters of this parasitoid varied with temperature (Bari et al. 2015).

In regards to mass rearing considerations of *T. zahiri*, the roles of host age preference, effect of supplementary diets, and alteration of the density of host eggs on the parasitism rate, fecundity, emergence rate, and adult longevity are not well understood. Parasitoid quality in mass rearing can be improved through knowledge of parasitoid biology, including larval development, adult longevity, and parasitism abilities (Bigler et al. 1991). Therefore, this study was undertaken to determine host age preference and effects of supplemental diet while manipulating host egg density on the percent parasitism, fecundity, and adult longevity of *T. zahiri* in the laboratory.

Materials and Methods

Host Age Preference

The choice test was conducted by placing rice hispa eggs of four age groups (age class—6 h, 24 h, 48 h, and 72 h) in a test tube (23 by 8 cm^2). Four rice leaf pieces having 10 hispa eggs from each of these four age groups were placed in each test tube with water-soaked cotton wool for maintaining leaf turgidity. The leaf pieces with different ages of rice hispa eggs were marked separately with permanent CD marker. A single female parasitoid, *T. zahiri*, was released in the test tube to parasitize the hispa egg according to its choice. The parasitoids were allowed to parasitize them for 24 h at about 25°C temperature in the laboratory, after which time the parasitoid was removed from the test tube arena. Both the ends of the test tube arena were covered by a black cloth except for the area where the eggs were placed. Dark shielding by the cloth forced the parasitoid to remain active around the more lit area of the test tube arena where the host eggs were available. The rice leaf with parasitized hispa eggs were kept in the test tubes for about 5 d, when the eggs were then examined under a microscope to determine the parasitism rate for each different age class of host eggs. The parasitized eggs were individually kept in a 5-ml glass vial and checked daily for adult emergence. The sex ratios of the emerged adults were determined. The experiment was replicated 10 times and 10 parasitoids were used in each time, where the source of parasitoids was laboratory.

Effects of Supplemental Adult Diets on Adult Longevity and Fecundity of *T. zahiri*

Freshly emerged *T. zahiri* were separated by sex and individually kept inside a test tube (23 by 8 cm^2). Twenty-five percent solution of honey, 25% sugar solution, host food (RH egg), host food + 25% honey, host food + 25% sugar solution, and water only were the different kinds of supplementary diets for the adult parasitoids.

Adult Longevity

An adult longevity experiment was conducted by captivating three cohorts of five male and five female adults of *T. zahiri* in five different test tubes. Five different supplemental diets, including a control (water as the diet), were provided for testing the effect on adult longevity of each *T. zahiri*. Every adult *T. zahiri* was treated as a unit of replication. If any of the adult parasitoids adhered to the water droplet or honey and sugar solution, that was discarded from the record. Survivorships of the parasitoid were recorded every 6 h until all parasitoids died.

Fecundity

To test the effect of different diets on the fecundity of *T. zahiri*, different types of diets were provided to each test individual in rearing chamber. After the death of the parasitoids, parasitized host eggs were separated and examined under a microscope to determine the parasitism and fecundity of the parasitoids. Individual parasitized eggs were kept in 5-ml glass vials with a few drops of water until adult emergence. The emerged adults were recorded and their sex ratios were also calculated.

Density-Dependent Parasitism

This part of the study was conducted by first allowing variable number of eggs to be parasitized by different numbers of parasitoids. Four numerical groups of hispa eggs having 10, 20, 30, and 40 eggs in a group were placed in different test tubes (size 23 by 8 cm^2) and allowed to be parasitized for 24 h by sets of 1, 2, 3, and 4 parasitoids, respectively, while maintaining a ratio of 1:10. As before, both the ends of the test tube were covered by the black cloth except the area where the eggs were present to promote exposure of the eggs in the lit area to the parasitoids.

In a second trial, a fixed number of 20 rice hispa eggs were kept in separate test tubes but this time exposed to 1, 2, 3, and 4 parasitoid number sets for 24 h. Again, both the ends of the test tube were covered by the black cloth except the area where the eggs were present. On removing the parasitoids after the stipulated time, the test tubes with the parasitoid eggs were kept in the laboratory at about 25°C, when after 5–6 d from exposure to a differently numbered set of parasitoids, the individual eggs from each set were placed separately in individual 5-ml vials in the laboratory until the emergence of the parasitoids. The unhatched eggs were dissolved in carbolxylene and alcohol (1:10) for 24 h and checked under the microscope to determine whether the eggs were parasitized. Four cohorts of 10 parasitoids were used in either trial. Thus, 40 individuals were tested where each individual was considered as one unit of replication.

Statistical Analysis

Data were analyzed by means of analyses of variance (one-way ANOVA), followed by Tukey's post hoc test at 0.05 level (SPSS, V. 19; 2011). The data of response variables were subjected to a logarithmic or arcsine transformation prior to analysis with a view to stabilize the variance and while also confirming that the back-transformed values were nonnegative.

Results

Host Age Preference of *T. zahiri*

In the choice experiment, *T. zahiri* equally parasitized 6- and 24-h-old eggs. However, percentage parasitism of 48- and 72-h-old eggs was significantly lower (Fig. 1; df = 17; $F = 17.11$; $P < 0.05$).

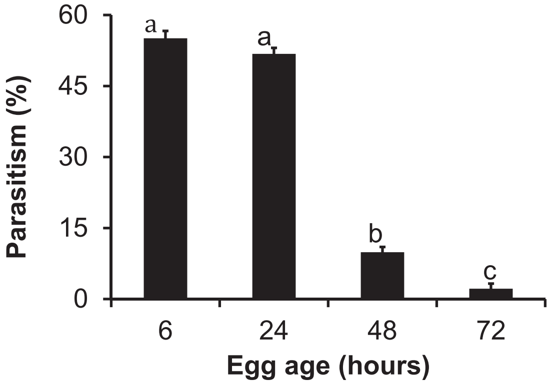

Fig. 1. Percent parasitism (mean ± SE) of 6-, 24-, 48-, and 72-h-old eggs of *D. armigera* by *T. zahiri* in a choice bioassay. Bars with different letters indicate significant differences between treatments ($n = 10$; df: 17; $P < 0.05$).

Number of parasitoids emerging decreased significantly with host egg age. The highest number of parasitoids developed from 1-d-old eggs, and the lowest number of parasitoids developed from 2- and 3-d-old eggs, respectively. However, sex ratio was not influenced by the age of the host eggs (Fig. 2, $P > 0.05$). In addition, developmental time from egg to adult did not significantly differ.

Adult Longevity of *T. zahiri* on Different Diets

Adult *T. zahiri* of both sexes showed a significant difference when exposed to different diets (Fig. 3). Males lived for 47.2–91.2 h with different diets. Significantly highest longevity (91.2 h) was found when 25% honey solution was provided with the host food and lowest in the control. Longevity of female *T. zahiri* ranged from 51.2 to 96.0 h on the different diets. Female longevity was 4–10 h longer than the male with similar diets. (Fig. 3). Longevity of both sexes was highest when the 25% honey solution was provided with the host food and was lowest in the control when only water was used as diet. No significant difference was observed in male and female longevity when 25% honey and sugar solutions were supplied separately with the host food. In both cases (for male and female), longevity was slightly higher in 25% honey solution than the 25% sugar solution.

Effect of Diets on the Parasitism and Fecundity of *T. zahiri*

Parasitism and fecundity of *T. zahiri* was studied on different diets. On an average 12.9–15.5 rice hispa eggs were parasitized when different diets were provided as food including control. No significant difference was found in the rates of parasitism, but the fecundity and emergence varied with diets (Fig. 4). Significantly highest fecundity and parasitoid emergence occurred when 25% honey solution was provided as diet with the host food followed by 25% sugar solution and the control. A single female *T. zahiri* laid highest number of eggs (38.5) with 25% honey solution and host food. The lowest fecundity (29.4 eggs) was found when only water was supplied with the host food. Adult emergence of *T. zahiri* reared on different diets ranged from 23.6 to 36.4%. Only 23.6 adults emerged in the treatments with water only (data not shown). On an average 1.8–2.8 parasitoids emerged from a single parasitized egg (data not shown). Significantly highest emergence occurred when 25% honey and 25% sugar solution were provided with host food as compared to control (Fig. 4). The sex ratio was always female biased (69–70%) in all the tested diets.

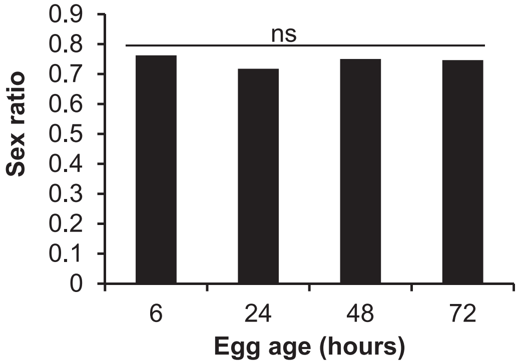

Fig. 2. Sex ratio (mean ± SE) of *T. zahiri* that emerged from 6-, 24-, 48-, and 72-h-old eggs of *D. armigera* parasitized in a choice bioassay. Bars with the same letters indicate nonsignificant differences between treatments ($n = 10$; df: 11; $P > 0.05$).

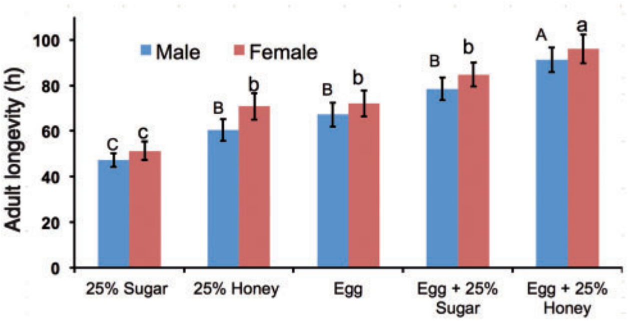

Fig. 3. Effect of host and supplementary food on the adult longevity of male and female *T. zahiri*. Bars with the same letters indicate nonsignificant differences between treatments ($n = 20$; df: 17; F for male 31.51; F for female 36.092; $P < 0.05$).

Density-Dependent Parasitism

The parasitism of *T. zahiri* varied significantly with the dependent of host densities (Fig. 5; Tables 1 and 2). *T. zahiri* showed increasing parasitism with increased host density and the trend was linear (Fig. 5). Results of two experiments with similar and variable parasitoid: host ratios showed that density of host eggs per parasitoid number influenced the rate of parasitism. In Table 1, mean parasitization was higher only with the 1 parasitoid:10 host egg combination, and on average, 7.90 eggs were parasitized when one parasitoid was released per 10 rice hispa eggs. When 20, 30, and 40 rice hispa eggs were offered to 2, 3, and 4 parasitoids, respectively, 6.6, 6.4, and 5.9 eggs were parasitized per parasitoid, respectively, and the result was statistically nonsignificant. Although the parasitoid: host ratio was similar, the small decreasing trend over means, may indicate some potential for mutual interference under some condition. The study also found that average parasitism efficiency per parasitoid decreased when more than one parasitoid was released on a fixed number of hosts (Table 2). Mean number of rice hispa egg parasitism decreased from 12.7 to 5.0 when parasitoid number increased from 1 to 4 in a small arena with fixed number of host (20 host eggs). Thus, when the parasitoid: host ratio differs among scenarios of exposure to host eggs, it was clearly indicated that mutual interference can happen (Tables 1 and 2). Therefore, a mass rearing protocol aimed at maximizing numbers of parasitoids to be reared for augmentative release, needs careful consideration with respect to parasitoid: host egg ratios.

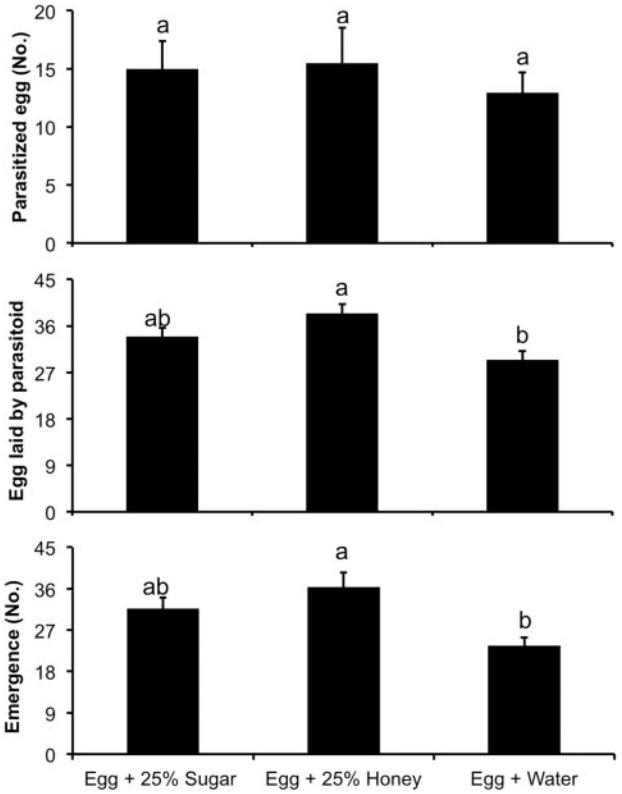

Fig. 4. Effect of diet condition on the parasitism performance and fecundity of *T. zahiri*. Bars with the same letters indicate nonsignificant differences between treatments ($n = 10$; df: 16; $P < 0.05$).

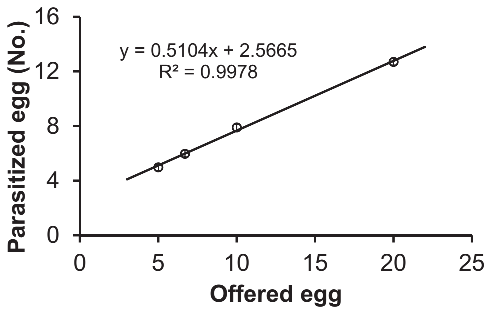

Fig. 5. Effect of *D. armigera* egg density on parasitism by *T. zahiri*.

Table 1. Number of rice hispa egg parasitized by *T. zahiri* in 24 h with similar parasitoid ratio

Parasitoid individuals and rice hispa eggs	No. of observations	No. of rice hispa eggs parasitized/parasitoid (mean ± SE)
1 parasitoid in 10 eggs (1:10)	40	7.90 ± 0.21a
2 parasitoid in 20 eggs (1:10)	40	6.58 ± 0.21b
3 parasitoid in 30 eggs (1:10)	40	6.37 ± 0.21b
4 parasitoid in 40 eggs (1:10)	40	5.93 ± 0.21b
Level of significance		*F*- value = 16.443 $P < 0.01$

Values within the column followed by different letter are significantly different at 5% by Tukey's post hoc test.

Table 2. Number of rice hispa egg parasitized by *T. zahiri* in 24 h with different parasitoid ratio

Parasitoid individuals and rice hispa eggs	No. of observations	No. of rice hispa eggs parasitized/parasitoid (Mean ± SE)
1 parasitoid in 20 eggs (1:20)	40	12.7 ± 0.23a
2 parasitoid in 20 eggs (1:10)	40	8.45 ± 0.23b
3 parasitoid in 20 eggs (1:6.7)	40	5.97 ± 0.23c
4 parasitoid in 20 eggs (1:5)	40	4.98 ± 0.23d
Level of significance		*F*- value = 222.10 $P < 0.01$

Mean values within the column followed by different letter are significantly different at 5% by Tukey's post hoc test.

Discussion

The two life history parameters of host species and host age are important considerations for an egg parasitoid (Liu et al. 1998). The host age is a limiting factor, as nutrient amount and quality of host egg decline as the host embryo develops. For this reason, old eggs are considered as a low-quality host food for mass rearing protocols of egg parasitoids. Parasitoids are unable to obtain nutrients from older host eggs, as the egg cuticle becomes harder with age (Strand et al. 1986), and parasitoids prefer fresh eggs to older ones to ensure that they get sufficient nutrients for maximal fecundity (Reznik and Umarova 1990, Monje et al. 1999, Romeis et al. 2000, Souza and Spence 2001, Tunçbilek and Ayvaz 2003, Da Rocha et al. 2006, Moreno et al. 2009).

Our study demonstrates that *T. zahiri* selected young hosts (1-d-old eggs) for parasitization. The old hosts (2- or 3-d-old eggs) were less preferred by *T. zahiri* and parasitized significantly fewer old eggs in no-choice assays (Fig. 1). The number of adult parasitoids developed from 2- and 3-d-old eggs was lower than that developed from 1-d-old eggs (data not shown). These findings support the possibility that *T. zahiri* females have a capacity to identify the most suitable hosts (1- > 2- > 3-d-old eggs) for producing their future generation. *T. zahiri* could discriminate 2- and 3-d-old eggs, and did not use these eggs for oviposition because old host eggs are not good in terms of their offspring development. Pyke et al. (1977) reported that parasitoids select the hosts which could support the best nutrition for their offspring development.

Sex ratio and total developmental time of *T. zahiri* were not influenced by host egg age (Fig. 2). Similar result was found when *T. remus* was tested (Penaflor et al. 2013). Though male population development from old hosts reduced development in *Tiphodytes gerriphagus* Marehal (Souza and Spence 2001), however it was not found in *Gryon gallardoi* (Brethes) (Da Rocha et al. 2006) and *Telenomus isis* Polaszek (Hymenoptera: Scelionidae) (Bruce et al. 2009). Sometimes perfect egg age for parasitoid selection for oviposition depends on host species, because embryonic development could differ among possible host species (Pak et al. 1986, Monje et al. 1999, Chabi-Olaye et al. 2001). *Trichogramma* is known to show great flexibility in parasitizing developed hosts within the egg (Pak 1986). In some *Trichogramma*, oviposition is restricted to the earlier stages of the host eggs within the first one-sixth or one-half of the host incubation periods (Juliano 1982). However, the percent parasitism is not strictly restricted but is <50% during half of the host incubation period (Pak and Oatman 1982). Host selection studies by *T. zahiri* on rice hispa egg clearly indicated that it is a parasitoid of younger eggs of the pest (Fig. 1). In a choice situation, *T. zahiri* showed a clear choice for 6- to 24-h-old eggs.

Longevity of male and female *T. zahiri* in the laboratory was found to be influenced by the feeding regime and was significantly higher with the presentation of either 25% sugar solution, 25% honey solution, or sugar and honey solution plus host food. Similar results were also observed by Haque (2001) who observed that longevity of *Leptomastix nr. epona* (Walker) was (four to five times) higher with the presence of honey solution, honeydew, and honey solution plus host food. Longevity of male and female *Metaphycus helvolus* (Compere) and *Microterys seyon* (Guerrieri) was significantly higher with the presence of 50% honey solution compared to other presented feeding regimes (Jahan 1997). A 50% solution of honey and honey dew influence the longevity of adult *L. nr. epona*, indicating that the availability of sugar-rich food would improve the control of *Pseudococcus longispinus* (Targioni-Tozzetti) by the parasitoid (Haque 2001). Reduction of host foraging time is an important factor for high reproductive performance of a parasitoid because if foraging time is minimal, more time to find their suitable host is available. Thus, availability of food sources for adult parasitoids in the target area has a strong effect on parasitism (Lewis et al. 1998).

Because adult parasitoids require food resources, they are not able to spend all of their time to explore hosts for oviposition but also need time to take care of their own short-term nutritional needs (Lewis et al. 1998). Parasitoids need to feed on carbohydrate-rich, nonhost foods for survival in the absence of suitable host foods. For example, when parasitoids are allowed to feed on carbohydrate-rich food (e.g., diluted honey solutions) they live significantly longer than those given only water (van Lenteren et al. 1987, Kim and Morimoto 1995). *Trichogramma zahiri* (Polaszek) lived longer on 25% sugar or honey solution than on water as the diet. Differences in male longevity on sugar and honey solutions were insignificant, but females lived longer on honey solution than sugar solution. When honey solution was provided along with host food, the longevity of *T. zahiri* was higher irrespective of sex. Females always lived longer than the males when they were provided with any particular diet; however, in this study, female longevity was significantly higher on honey solution alone or when in combination with host food, than on sugar solution or with honey in combination with sugar solution.

The type of sugar source also influenced the longevity of *Trichogramma* (Leatemia et al. 1995). Honey is commonly used as a food source for the study of *Trichogramma* longevity, but very few reports show the effect of other sugar sources. For an example, in case of *T. platneri* (Nagarkatti) fructose was better than other source sugars (Leatemia et al. 1995). David et al. (1987) reported that higher adult longevity was found in *T. chilonis* (Ishii) when they were fed with only sugar than with different proteins along with glucose. When *T. platneri* was reared with water-fed or unfed, the average adult longevity was 2 d less than that of a sugar supply at 25°C (McDougall and Mills 1997). Similar effects were found in other *Trichogramma* species (Smith et al. 1986, Hohmann et al. 1988).

Increasing densities of female parasitoids resulted in reduced parasitoid efficiency if parasitoid: host ratio differs. It clearly indicates that the mean parasitism by the individual parasitoid *T. zahiri* decreased due to mutual interference as that ratio is altered. In this case, parasitoids might rapidly recognize other fresh eggs nearby and start to parasitize them, which leads to a reduction in time spent searching for new hosts and an increased tendency for dispersal. The same tendency may also be observed after a female detects a host that has already been parasitized (Hassel and Waage 1984). Interference is designated as a density-dependent factor which is found in parasitoids (Hassel and Waage 1984). The attack rate of *Anisopteromalus calandrae* (Howard) reduced in curvilinear fashion with the increase of parasitoid numbers, demonstrating mutual interference. Total number of offspring remained similar when the density of conspecifics increased from 8 to 20. Superparasitism was observed in *A. calandrae* with low host density; however, the superparasitism rate was lower than that of *L. distinguendus* due to strong mutual interference (Ryoo et al. 1996). Similarly, in the density-dependent parasitism study of this paper, the *T. zahiri* mutual interference decreased the mean number of host egg parasitized by an individual parasitoid, although the total number of parasitized eggs increased.

Adult longevity of *Trichogramma* is affected by various factors including food (Leatemia et al. 1995). In this study, we disclose the effect of host egg age and supplementary food on the total performance of *T. zahiri* in laboratory studies to facilitate future mass culture commercialization of this effective egg parasitoid.

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