Estimating development rate and thermal requirements of *Hemiptarsenus zilahisebessi* (Hymenoptera: Eulophidae) Parasitoid of *Liriomyza sativae* (Diptera: Agromyzidae) using linear and non linear models

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ABSTRACT. The temperature-dependent development of *Hemiptarsenus zilahisebessi* Erdös (Hymenoptera: Eulophidae), a biological control agent of *Liriomyza sativae* Blanchard (Diptera: Agromyzidae), was studied in the laboratory at seven constant temperatures (10°C, 15°C, 20°C, 25°C, 30°C, 35°C, and 40°C) with a relative humidity of 65% and a photoperiod of 16L:8D h.. The total developmental time (egg to adult) decreased significantly with increasing temperature, and there was no development at 10°C or at 40°C. Linear and nonlinear models were used to describe the relationship between developmental rate (1/days) and temperature (°C), and to determine developmental thresholds. Using a linear model, the lower temperature threshold (zero development) was estimated to be 8.94°C for males and 9.02°C for females, and the thermal constant (K) was 147.1 degree-days (DD) for males and 156.3 DD for females. Among the nonlinear models examined, the Briere-1 and Briere-2 models were accepted on the basis of goodness-of-fit to the data (residual sum of squares and coefficient of determination) and estimable temperature thresholds (T_0, T_{opt} and T_{max}). These models gave the best description of the temperature-dependent development of *H. zilahisebessi*. Temperature-based development models can be useful in designing mass-rearing protocols, in helping to make decisions in augmentative release trials, and in the development of predictive modelling.

INTRODUCTION

The vegetable leafminer *Liriomyza sativae* Blanchard is a polyphagous pest worldwide, causing economic damage to vegetable crops and ornamental flowers (PARRELLA 1983, SPENCER 1986, REITZ & TRUMBLE 2002, LEE et al. 2005). Females of *L. sativae* puncture the upper leaf surface for feeding and oviposition. The larvae feed in the leaf mesophyll tissue and form a serpentine mine; thereby reducing the photosynthetic capacity of leaves (MINKENBERG & HELDERMAN 1990, PETITT & WIETLISBACH 1994). At high densities of *L. sativae* this feeding can severely reduce yields and/or kill the plants (JOHNSON et al. 1980b, SAITO et al. 1995).

Chemical insecticides have been used for many years and are still the main tools for controlling *Liriomyza* leafminers in Iran and many other countries. Because *L. sativae* has developed a great resistance to pesticides, commercially available parasitoids have been used as effective biological control methods in greenhouses (JOHNSON et al. 1980a, PARRELLA 1987, HEINZ et al. 1993, SAITO et al. 1997, KASPI & PARRELLA 2005). There are many hymenopteran parasitoids that attack *L. sativae*, and *Hemiptarsenus zilahisebessi* Erdös has been suggested as a promising agent (MURPHY & LASALLE 1999, FATHIPOUR et al. 2006). However, relatively few studies have examined the basic biology of this parasitoid (HYUNGCHEOL et al. 2002). *H. zilahisebessi* has been recognized recently as an effective biological control agent of leafminers such as *L. sativae*. In Iran, the leafminer parasitoids *Digluphus isaea* (WALKER) and *H. zilahisebessi* are the most important and frequent species on cucumber (FATHIPOUR et al. 2006), and have an important role in the suppression of *L. sativae* (PARRELLA 1987, HEINZ et al. 1993). Biological control in a framework of integrated pest management (IPM) is essential to reduce leafminer populations effectively (NEALIS et al. 1984, MINKENBERG & VAN LENTEREN 1986, MINKENBERG 1989).

Indigenous natural enemies of *Liriomyza* spp., particularly parasitoids, are diverse within their native ranges and there is evidence that these can regulate leafminers in pesticide-free areas. They can also be diverse in their adventive ranges in continental areas, as invading *Liriomyza* spp. quickly attract local parasitoids and other polyphagous arthropod predators (MURPHY & LASALLE 1999). When natural control by these parasitoids does not provide adequate suppression of leafminers, augmentative biological control is a potential solution (MINKENBERG & VAN LENTEREN 1987, BADER et al. 2006).

Degree-days (DD) is the acquisition of thermal units over time above a critical minimum for which development is required, and this parameter has been used to predict many aspects of insect life history. This physiological approach can assist in the calculation of the number of generations that an insect could be expected to have over a specific period of time (PILKINGTON & HODDLE 2006). The ability to accumulate sufficient DD to complete development in a new area may indicate how vulnerable that region is to invasion by an exotic organism (SUTHERST 2000), and whether incursion will be transient due to unfavor-

able conditions for prolonged periods (HATHERLY et al. 2005) or potentially permanent due to year-round conditions favorable for growth and reproduction (SUTHERST 2000).

DD can be a valuable tool for predicting the development, occurrence, number of generations and population dynamics of insects. Insect development occurs only between an upper and a lower temperature threshold (KONTODIMAS et al. 2004); i.e. there is no development at temperatures below the lower threshold or above the upper threshold (GILBERT & RAWORTH 1996, ROY et al. 2002, HAGHANI et al. 2007b).

The objective of this study was to determine the developmental threshold and the thermal requirements of immature stages of *H. zilahisebessi* reared on *L. sativae* at seven constant temperatures between 10°C and 40°C. Our goal was to construct a model of development for this parasitoid to be used in a comprehensive IPM of vegetable leafminer on cucumber.

MATERIAL AND METHODS

Culture of the host and parasitoid

The vegetable leafminer *L. sativae* and its parasitoid *H. zilahisebessi* were collected originally from cucumber grown in a greenhouse in Tehran, Iran in July 2004. *L. sativae* was reared on *Phaseolus vulgaris* L. variety Sunray at 25(± 1) °C with a relative humidity of 65(± 5) % and a 24 h cycle of 16L:8D h. A colony of *H. zilahisebessi* was established on the beans. Flies and wasps collected in the wild were regularly added to the colony to reduce the effects of inbreeding. *Cucumis sativus* L. variety Negin was grown to the 5–7 leaves stage (the top and the two lowest leaves were removed), and the leafminer and parasitoid were reared in the laboratory for several generations before the experiments reported here.

Experimental conditions

The development time (days) of *H. zilahisebessi* was studied at constant temperatures 10°C, 15°C, 20°C, 25°C, 30°C, 35°C, and 40°C in growth chambers with a relative humidity of 65(± 5) % and a photoperiod of 16L:8D h. At each temperature, plants containing 6 or 7 *Liriomyza* larvae (late second to early third instar) per leaf and 25–30 *H. zilahisebessi* adult females were kept in transparent plastic cages covered at the top with organza. Female parasitoids were allowed to attack the leafminer larvae for 4–6 h in a growth chamber at 25(± 1) °C, with a relative humidity of 65(± 5) %. After removing the adult parasitoids, plants with parasitized larvae were left to develop at a constant temperature (see above). The development of the immature parasitoids was observed daily until adults emerged.

Temperature-dependent models

Estimation of thermal parameters was performed by the method of thermal summation based on the linear portion of the temperature–developmental rate relationship (BERNARDO et al. 2006). Developmental rate $1/D$ was fit with temperature from 10°C to 35°C to obtain the relationship in terms of $1/D = a + bT$, where D is the developmental period (in days), T is the temperature (in °C), and a and b are the regression parameters. The lower temperature threshold ($T_0 = -a/b$) and the thermal constant ($K = 1/b$) were calculated by extrapolating the linear portion of the temperature–development curve.

The relationship between temperature and development rate was also fit in the whole range of investigated temperatures by nonlinear development rate models, chosen because they are the most commonly used for that purpose. The five nonlinear models were: one described by LOGAN et al. (1976); two described by LACTIN et al. (1995), and two described by BRIERE et al. (1999).

Evaluation of the models was done on the basis of the following criteria: fit to the data; number and biological value of the fitted coefficient; number of measurable parameters; and accuracy of the estimation of the thresholds. The model should describe the data accurately. The residual sum of squares (*RSS*) and the Akaike information criterion (*AIC*) were used to evaluate the goodness-of-fit. A good model must explicitly include smaller values of *RSS* (ROY et al. 2002, KONTODIMAS et al. 2004) and *AIC* (AKAIKE 1974).

Using the coefficient of determination (R^2) value to discriminate between models with different numbers of parameters is invalid, because models with more parameters will always provide a better fit. We used *AIC*, which is an independent parameter (VUCETICH et al. 2002) defined as:

$$AIC = n \ln\left(\frac{SSE}{n}\right) + 2P$$

where n is the number of observations and P is the number of model parameters including the intercept, and *SSE* is the sum of squares for the model error term.

The model should allow estimation of parameters with biological significance (BRIERE et al. 1999, ROY et al. 2002, 2003). For development, the key biological parameters are the low temperature threshold, the optimal temperature, and the high temperature threshold (ROY et al. 2002).

The developmental rate ($1/D$) is the reciprocal of development time (D) and values range between 0 and 1. These rates are used in models of developmental rate summation in which daily estimates of developmental rates are needed. The development of an organism is completed when the sum of its daily developmental rates reaches the value of 1 (CURRY & FELDMAN 1987, ZAMANI et al. 2007).

Statistical analysis

Data satisfying conditions of normality and homoscedasticity were analyzed by one-way ANOVA and the means were separated at the $P \leq 0.05$ level of significance by the least significant difference test. The temperature-dependent models were analyzed with the Levenberg-Marquardt algorithm using SPSS statistical programs (GREENBERG et al. 2000).

RESULTS

Development time

Mean developmental time and developmental rate of each immature stage at constant temperature are shown in Table 1. The period of immature development (oviposition to adult emergence) decreased significantly with increasing temperature between 15°C and 35°C, and there was no development below 10°C or above 40°C; i.e. 10°C and 40°C are outside the lower and upper developmental threshold, respectively.

Male parasitoids developed faster than females at all temperatures tested. Male parasitoids often develop faster than females and emerge from the host earlier. This phenomenon is called protandry, which is known to exist in many insect species, including *H. zilahisebessi* and most parasitic Hymenoptera (QUICK 1997). At 15°C and at 35°C, the total pre-imaginal development time ranged from 24.6 days and 6.1 days for males and 25.8 days and 6.4 days for females, respectively (Table 1).

Model evaluation

The linear model is recommended for the description of temperature-dependent development of of *H. zilahisebessi* at 10-35°C. In this case, only the data obtained at 10°C, 15°C, 20°C, 25°C, 30°C and 35°C were used in calculations because we wanted to focus on the linear part of the correlation between temperature and rate of development. The regression *P*-value showed a high linear relationship between temperature and developmental rate of this species at 10–35°C (Table 2).

Using the linear model, the lower temperature threshold (T_0) for pre-imaginal development of *H. zilahisebessi* was found to be 8.94°C for males and 9.02°C for females, and the thermal constant *K* was 147.1 DD for males and 156.3 DD for females. Our findings indicated that male wasps had the lowest temperature threshold and required fewer degree-days than females for completing their development (Table 2).

Data were fitted to various nonlinear temperature-dependent models. The values of parameters estimated for developmental rate by nonlinear models for males and females of *H. zilahisebessi* are presented in Table 2. According to the values of *RSS* and *AIC* and temperature thresholds, there was no substantial difference between the models. The lower temperature threshold (T_0) was underestimated by Lactin-2 (8.25°C for males and 7.92°C

for females) and it seems that this model did not predict the development rate of *H. zila-hisebessi* accurately. The Briere-1 and Briere-2 models estimated the lower temperature threshold to be 9.86°C and 9.82°C for males, and 10.19°C and 10.05°C for females, respectively (Table 2). The Logan-6 and Lactin-1 models could not estimate a lower temperature threshold (T_0) because these models predict a positive development rate even at 0°C. The curves of the influence of temperature on the development rate of *H. zilahisebessi* for the Briere-1 and Briere-2 models are shown in Figure 1.

Table 1. Development time (mean±SE) and development rate of *H. zilahisebessi* in the presence *L. sativae* reared on cucumber at 15°C, 20°C, 25°C, 30°C, and 35°C.

Sex	Temperature (°C)[*]				
	15	20	25	30	35
Male					
n	26	24	27	23	28
Development time	24.6±0.16 a	12.8±0.08 b	8.5±0.11 c	6.7 ±0.10 d	6.1±0.06 e
(Range)	(24-26)	(12-13)	(8-9)	(6-7)	(6-7)
Development rate	0.041	0.078	0.118	0.149	0.164
Female					
n	28	21	27	29	25
Development time	25.8±0.13 a	13.7±0.10 b	9.1±0.06 c	7.2±0.08 d	6.4±0.10 e
(Range)	(25-27)	(13-14)	(9-10)	(7-8)	(6-7)
Development rate	0.039	0.073	0.110	0.139	0.156

Means in same row followed by the same small letters are not significantly difference. All significant differences identified by the LSD test at the 0.05 level.

[*]No development occurred at 10°C and 40°C.

Table 2. Estimated parameters of development rate nonlinear models for describing total development of *H. zilahisebessi* reared on *L. sativae*.

Model	Equation	Parameters	Estimates Male	Estimates Female
Linear	$D(T) = a + bT$	a	-0.0608	-0.0577
		b	0.0068	0.0064
		T_0	8.94	9.02
		K	147.1	156.3
		AIC	-54.62	-56.89
Logan-6	$D(T) = \Delta \times \left[e^{\rho.T} - e^{(\rho.T_{max} - \frac{T_{max}-T}{\Delta T})} \right]$	T_{max}	39.99	40
		T_{opt}	33.35	33.34
		RSS	0.72×10^{-3}	0.63×10^{-3}
		AIC	-60.31	-61.21
Lactin-1	$D(T) = e^{\rho.T} - e^{\left(\rho.T_{max} - \left(\frac{T_{max}-T}{\Delta T}\right)\right)}$	T_{max}	39.99	39.94
		T_{opt}	33.33	34.36
		RSS	0.72×10^{-3}	1.85×10^{-3}
		AIC	-60.31	-53.66
Lactin-2	$D(T) = e^{\rho.T} - e^{\left(\rho.T_{max} - \left(\frac{T_{max}-T}{\Delta T}\right)\right)} + \lambda$	T_0	8.25	7.92
		T_{max}	40.67	40.60
		T_{opt}	32.56	32.67
		RSS	0.31×10^{-3}	0.32×10^{-3}
		AIC	-64.26	-63.90
Briere-1	$D(T) = a \times T(T - T_0) \times (T_{max} - T)^{1/2}$	T_0	9.86	10.19
		T_{max}	40.00	40.00
		T_{opt}	33.16	33.19
		RSS	0.17×10^{-3}	0.22×10^{-3}
		AIC	-68.41	-66.53
Briere-2	$D(T) = a \times T(T - T_0) \times (T_{max} - T)^{1/m}$	T_0	9.82	10.05
		T_{max}	40.00	40.00
		T_{opt}	32.44	32.30
		RSS	0.24×10^{-3}	0.33×10^{-3}
		AIC	-65.88	-63.66

In linear model, a is intercept, b is slope, T is temperature, T_0 is low temperature threshold, K is thermal constant.

In Logan-6 model, T is the rearing temperature (°C), Δ is the maximum developmental rate, ρ is a constant defining the rate of optimum temperature, T_{max} is the lethal maximum temperature, ΔT is the temperature range over which physiological breakdown becomes the overriding influence.

In both Lactin-1 and Lactin-2 models T, ρ, T_{max} and ΔT are as in the Logan-6 model, and in the Lactin-2 model λ forces the curve to intercept the Y-axis at a value below zero and thus allows estimation of a low temperature threshold.

In both Briere-1 and Briere-2 models T is the rearing temperature (°C), a is an empirical constant, T_0 is the low temperature development threshold, T_{max} is the lethal temperature threshold, and in the Briere-2 model 'm' is an empirical constant.
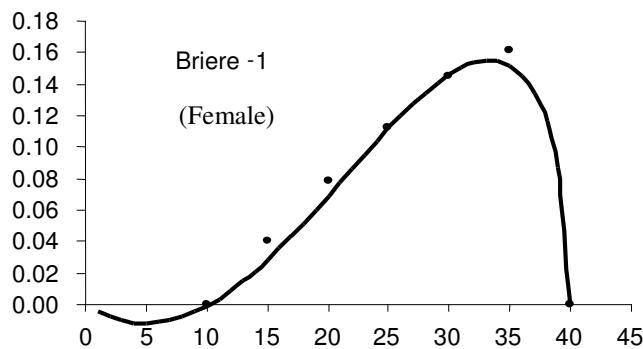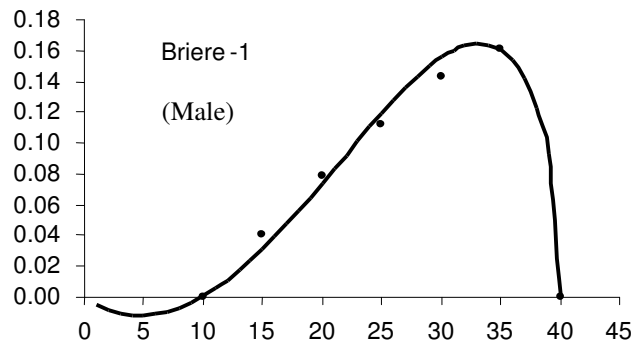
Fig 1. Fitting Briere-1 model to observed values of total development rate (1/D, in days^{-1}) of *H. zila-hisebessi* versus temperature (°C) in males and females. Dots represent observed data. In all charts, the ordinate is the rate of development and the abscissa is the temperature.

DISCUSSION

As far as we know, there is no other study in which a temperature threshold for development of immature *H. zilahisebessi* on *L. sativae* reared on cucumber has been estimated. A brief description of *H. varicornis* biology when reared on *L. trifolli* has been given (ARAKAKI & KINJO 1998). According to the study described by SAITO et al. (1997), the egg to adult development time of males and females of *H. varicornis* at 25°C was 8.6 days and

8.8 days on *L. trifolii*, and 8.8 days and 9.0 days on *L. bryoniae*, respectively. The lower temperature threshold for development of the males and females of *H. varicornis* was estimated by linear regression to be 8.9°C and 8.5°C on *L. trifolii*, and 8.2°C and 8.4°C on *L. bryoniae*. HONDO et al. (2006) calculated a regression equation for egg to adult development of *H. varicornis* on *L. trifolii* that was quite different from that reported by SAITO et al. (1997). BORDAT et al. (1995) have provided information on parasitism of different stages of *L. trifolli* larvae by *H. varicornis*.

Given the wide range of linearity in the developmental rate curves, the degree-day concept may be useful in predicting the development *of H. zilahisebessi*. Temperatures above 35°C may decrease the developmental rate of this wasp or even prevent it.

Nonlinear models were fitted to the data of the current study giving small *RSS* and *AIC*. The Logan-6 and Lactin-1 models cannot estimate T_0, while the Lactin-2 model did not provide a realistic estimate of T_0. The Briere-1 and Briere-2 models are more suitable for estimating temperature thresholds (T_0, T_{opt} and T_{max}), and best describe the correlation of the development rate of *H. zilahisebessi* and temperature. We obtained the same results for another hymenopteran parasitoid, *D. isae*, on *L. sativae* (HAGHANI et al. 2007a). It should be noted that the linear equation was a good fit to the experimental data, and it was the easiest to calculate. Moreover, it is the only equation that enables calculation of the thermal constant.

Laboratory estimations of DD requirements and net reproductive rate can be used to determine what range of temperature is suitable for sustained population growth (PILKINGTON & HODDLE 2006). An understanding of how temperature ranges affect estimates of population growth of an invading or deliberately introduced biological control agent can aid the prediction of invasion success by indicating geographical areas where unfavorable temperature conditions may prevent the establishment of permanent populations (HOELMER & KIRK 2005).

Thermal characteristics vary among species, populations and developmental stages (HONEK 1999), and the rate of development is influenced by factors other than temperature, such as nutrition, humidity, and photoperiod, which should not be neglected in the application of the models (GILLBERT & RAWORTH 1996).

The results of this study provide some essential information on the biology of *H. zilahisebessi*, which may allow better use of this species as a control agent of *L. sativae* on cucumber. Also, they could be incorporated into models taking into consideration additional information on rates of parasitism and reproduction. Temperature-based developmental models can be used to predict the occurrence, the number of generations, and possibly the population dynamics of *H. zilahisebessi* on *L. sativae* in the cucumber. These models will be of use in monitoring this wasp and be valuable in the implementation of pest management programs. Experiments done under fluctuating temperature conditions might provide more accurate information about what occurs in the field.

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