Temperature-dependent development of *Habrobracon hebetor* (Hym.: Braconidae) reared on larvae of *Galleria mellonella* (Lep.: Pyralidae)

M. Forouzan[1], M. Amirmaafi[2] and A. Sahragard[3&*]
1. Department of Plant Protection, West Azerbaijan Agricultural Research and Natural Resources Centre, Agricultural Research and Education Organization, 2. Iranian Research Institute of Plant Protection, Tehran, Iran, 3. Department of Plant Protection, Agricultural College, Guilan University, Rasht, Iran.
*Corresponding author, E-mail: sahragard@guilan.ac.ir

Abstract

The development times and the survival rates of different stages of *Habrobracon hebetor* Say reared on the last instar larvae of *Galleria mellonella* (L.) were compared at ten different constant temperatures (16 - 38 ºC). The development time of immature stages of the parasitoid, *H. hebetor*, decreased as the temperature increased in the range of 16 to 38 ºC. However, no larvae could survive and develop at 16 ºC. Development time from egg to adult females was the shortest (8.368 ± 0.069 days) at 35 ºC and the longest (32.667 ± 0.33 days) at 18 ºC. Egg incubation period, larval and pupal development times were significantly different at various constant temperatures. No significant difference was found between two sexes in their developmental periods from eggs to adult stage. The survival rate of the egg stage ranged between 94.90 and 100% at all temperature levels, but larval survival rates was significantly different at various temperatures. Although significant difference was found in the survival rate of pupal stage ($P < 0.05$), the trend of survival rate for pupae was similar to those of larvae. The relationship between temperature and the developmental rate of the parasitoid well described by linear regression model ($R^2 = 0.89$, $P = 0.0001$, at the egg stage and $R^2 = 0.95$, $P = 0.0001$, at the egg-adult stage). The lowest threshold temperature was obtained for all developmental stages of the parasitoid. Degree-days requirements (DD) for egg, larva, pupa and egg-female stages were 22.73, 56.82, 109.89 and 188.68, respectively. The results in this study showed that the temperature range between 25 and 32 ºC provide a favourable condition for mass rearing of this parasitoid.

Key words: *Habrobracon hebetor*, *Galleria mellonella*, developmental rate, survival rate, threshold temperature, degree-day requirements

چکیده

دوره‌های رشد و نرخ بقای *Habrobracon hebetor* Say پرورش‌یافته روی سن آخر لاروی *Galleria mellonella* (L.) در ۱۰ دمای مختلف و ثابت (از ۱۶ تا ۳۸ درجه‌ی سانتی‌گراد) مورد مقایسه قرار گرفت. دوره‌های رشد مراحل نابالغ زنبور پارازیتوئید در دامنه‌ی دمایی ۱۶ تا ۳۸ درجه‌ی سانتی‌گراد با افزایش دما کاهش یافت. با وجود این، در دمای ۱۶ درجه‌ی سانتی‌گراد هیچ لاروی قادر به ادامه‌ی حیات و رشد نبود. زمان رشد از تخم تا ماده‌های بالغ در دمای ۳۵ درجه‌ی سانتی‌گراد کوتاه‌ترین (۰/۰۶۹ ± ۸/۳۶۸ روز) و در دمای ۱۸ درجه‌ی سانتی‌گراد طولانی‌ترین مدت (۰/۳۳ ± ۳۲/۶۶۷ روز) را داشت. دوره‌ی تفریخ تخم، دوره‌های لاروی و شفیرگی در دماهای ثابت مختلف دارای تفاوت معنی‌دار بودند. بین دوره‌های رشدی از تخم تا مرحله‌ی بلوغ در حشرات نر و ماده تفاوت معنی‌داری مشاهده نشد. نرخ بقای مرحله‌ی تخم در تمام سطوح دمایی بین ۹۴/۹۰ و ۱۰۰ درصد در نوسان بود، ولی نرخ بقای لاروی در دماهای مختلف دارای تفاوت معنی‌دار بود. اگر چه در نرخ بقای دوره‌ی شفیرگی، تفاوت معنی‌دار بود (p < ۰/۰۵)، روند نرخ بقای شفیره‌ها شبیه نرخ بقای دوره‌ی لاروی بود. رابطه‌ی بین دما و نرخ رشد پارازیتوئید به خوبی با مدل رگرسیون خطی برازش یافت (P = ۰/۰۰۰۱، R^2 = ۰/۸۹ در مرحله‌ی تخم و P = ۰/۰۰۰۱، R^2 = ۰/۹۵ در مرحله‌ی تخم- بالغ). پائین‌ترین آستانه‌ی دمایی برای همه‌ی مراحل رشد پارازیتوئید به دست آمد. نیازهای دمایی تخم، لارو، شفیره و از تخم تا حشرات ماده به ترتیب ۲۲/۷۳، ۵۶/۸۲، ۱۰۹/۸۹ و ۱۸۸/۶۸ روز- درجه بود. نتایج این مطالعه نشان داد که دامنه‌ی دمایی بین ۲۵ و ۳۲ درجه‌ی سانتی‌گراد شرایط مناسبی را برای پرورش انبوه این پارازیتوئید فراهم می‌آورد.

واژگان کلیدی: *Habrobracon hebetor*، *Galleria mellonella*، نرخ رشد، نرخ بقا، آستانه‌ی دمایی، نیازهای روز- درجه

Introduction

Habrobracon hebetor Say is an idiobiont and gregarious larval ectoparasitoid of many moths (Quicke & Van Achterberg, 1990). The parasitoid has been collected and reported by Farahbakhsh (1961) from Varamin, Iran for the first time, and it is now used as a biological control agent in the control of larvae of lepidopteran pests in cotton, tomato, soybean, and corn fields (Anonymous, 2003). The relationship between temperature and insect development time and developmental rate has been investigated by various research workers. This relationship was established very early and represents an important ecological variable for modelling population dynamics of insects (Uvarov, 1931; Davidson, 1944; Richards, 1957; Howe, 1967; Gilbert & Raworth, 1996; Jarosik *et al*., 2002). Temperature is an important factor in the development of immature parasitoids. It is clear that parasitoid development is prolonged and mortality increases at relatively cool and hot temperature extremes (Cheah, 1987; Cave & Gaylor, 1988). Also, the phenology and synchrony of the parasitoid-host relationship is affected by temperature (Dowell, 1979). Developmental rate is the reciprocal of development period in days. These rates are used in development models where data are added daily. Development is completed when the sum of their daily developmental rates reaches 1 (Curry *et al*., 1978). The exact estimation of the growth and development rates of insect pests and their natural enemies is undoubtedly of peculiar importance in the development of programs aimed at their control, and the application of phenological models in the integrated pest management programs has considerably increased in recent decades (Wagner *et al*., 1984; Worner, 1991).

It has been argued that the degree-days models suffice to predict insect development in the field, and the use of nonlinear models is not necessary (Campbell *et al*., 1974; Gilbert, 1988). This argument may well apply to many insects whose development and reproduction are practically confined to temperatures within the linear regions of the development curves, especially for those insects that enter diapause or emigrate in anticipation of unfavourable conditions (Gilbert & Raworth, 1996). The linear approximation enables the estimation of lower developmental threshold and thermal constant within a limited temperature range, usually 15-30 ºC (Honek, 1999). Linear model has been used widely, because it needs minimal data for formulation, it is very easy to calculate and apply, and it usually results in approximately correct values with negligible differences in accuracy from more complex models (AliNiazee, 1976; Obrycki & Tauber, 1981; Briere *et al*., 1999; Jarosik *et al*., 2002).

Moreover, it is the simplest and easiest method for estimation of the thermal constant (Worner, 1992), as it includes few parameters and with clear biological content, it is, therefore, an important step toward a better understanding of the biology and population dynamics of insect pests (Muniz & Nombela, 2001). Linear models have been used by Lopez *et al*. (2001), Tobin *et al*. (2001), Liu & Tsai (2002), Kontodimas *et al*. (2004) and Krugner *et al*. (2007) to estimate stage-specific base temperature thresholds and degree-day requirements of insects.

Development in *H. hebetor* is not well studied. The only study on the effect of temperature on developmental rate of this parasitoid is that of Adashkevich & Saidova (1987), where they estimated the lower and upper temperature thresholds as 12.4 and 37.8 ºC, respectively. They also determined thermal requirements from egg to adult as 186.7 degree days. Amir-Maafi & Chi (2006) also studied the demography of this parasitoid on two pyralid host species *Galleria mellonella* (L.) and *Ephestia kuehniella* Zeller.

The objectives of this study were to establish the developmental threshold and degree-day requirements for *H. hebetor*. These data allow the selection of appropriate temperatures for the rearing of this parasitoid under laboratory conditions.

Materials and methods

The research on temperature-dependent development of immature stages of *H. hebetor* was carried out at ten constant temperatures (16, 18, 20, 23, 25, 28, 30, 32, 35, and 38 ºC) with a photoperiod of 16 h and a relative humidity of 60 ± 5 % under laboratory conditions. A colony of *H. hebetor* reared on the larvae of *G. mellonella* was used in this study (Amir-Maafi & Chi, 2006). The experiments were initiated with a total number of 1400-2600 (0-1 h) eggs of the parasitoid at each level of temperature. An individual larva of *G. mellonella* bearing an egg of the parasitoid was selected randomly and placed in a ventilated plastic Petri-dish (5 cm in diameter) lined with a piece of tissue paper. Petri-dishes were observed at 4-h intervals at the egg stage and 24-h intervals at the larval stage to record their development.

Linear regression was used to analyze relationship between developmental rate of *H. hebetor* and temperature. The linear regression was Y = a + bX, (1), where "Y" is the developmental rate at each temperature level, "a" is the intercept, "b" is the slope of the line and "X" is the temperature.

The degree-day (DD) was obtained for all growth stages of the parasitoid using the following formula (Campbell *et al*., 1974): DD = 1/b, (2). The threshold temperature or developmental threshold (T_0) was calculated using the following relationship: $T_0 = -a/b$, (3).

The rate of survival for each developmental stage was obtained by dividing the number of individuals survived at the end of a stage on its total number at the beginning of the experiment. Prior to the analysis of variance, survival rates were transformed using $(x + 0.5)^{1/2}$ formula. Data analysis was done with SAS 6.12. Duncan's Multiple Range Test was used to compare the means if there were any significant differences among treatments.

Results

The study of development time and survival rate of different growth stages of *H. hebetor* showed that the parasitoid was able to complete its life cycle at all temperature levels except for 16 ºC. Development time of all stages of this parasitoid was affected by temperature; it decreased as temperature increased (table 1). The incubation period lasted from 0.815 ± 0.024 days (n = 1440) at 38 ºC to 6.27 ± 0.124 days (n = 2570) at 16 ºC. Larval development time ranged between 2.549 ± 0.076 (n = 1170) and 11.405 ± 0.198 days (n = 120) at 32 ºC and 18 ºC, respectively. No larvae could survive and develop at 16 ºC.

Table 1. Mean development times (in days) of immature stages of *H. hebetor* reared on *G. mellonella* larvae at different temperatures (with a RH of 60 ± 5% and 16:8 h L:D).

Temperature	Development time (Mean ± SE)				
(ºC)	Eggs	Larvae	Pupae	Egg to female	Egg to male
16	6.27±0.124a	0. 00f	0. 00f	0. 00	0. 00
18	2.595±0.076b	11.405±0.198a	19.5±0.815a	32.667±0.33a	33.857±1.299a
20	3.664±0.073b	6.237±0.128b	17.463±0.202b	27.889±0.087b	26.667±0.029b
23	1.524±0.37c	6.232±0.159 b	9.454±0.062c	17.429± 0.291c	17.083±0.216c
25	1.542±0.42c	4.675±0.11c	8.369±0.098c	14.385±0.14 d	14.75±0.17d
28	1.767±0.29c	3.429±0.032d	6.895±0.054d	12.078±0.096e	12.121± 0.136e
30	1.47±0.43c	2.079±0.039c	6.791± 0.109d	11.000±0.17e	11.1± 0.143e
32	0.969±0.63c	2.549±0.076 e	5.826±0.023de	9.333±0.104f	9.37±0.166f
35	1.00±0.00c	3.012±0.088de	4.417±0.063e	8.368±0.069f	8.6±0.134f
38	0.815±0.024c	2.815±0.073e	5.156±0.028e	8.489±0.011f	8.455±0.152f

Means within each column followed by the same letter are not statistically different by Duncan's Multiple Range Test (P = 0.05).

Pupal period was also affected by temperature as the shortest and longest development times were 4.417 ± 0.063 (n = 770) and 19.5 ± 0.815 days (n = 100) at 35 ºC and 18 ºC, respectively.

Egg to adult development time of females was the shortest (8.368 ± 0.069 days) (n = 490) at 35 ºC and the longest (32.667 ± 0.33 days) (n = 30) at 18 ºC. This period for males was

8.455 ± 0.152 days (n = 220) at 38 ºC and 33.857 ± 1.299 days (n = 70) at 18 ºC. Egg incubation period, larval and pupal development times were significantly different at various constant temperatures ($P < 0.05$). No significant difference was found between two sexes in their developmental periods from eggs to the adult stage.

The survival rate of egg stage ranged between 94.9 and 100% at all temperature levels. Egg survival was not significantly different among temperatures ranging from 16 to 38 ºC ($P > 0.05$), but larval survival rates were significantly different at various temperatures ($P < 0.05$). Larvae could not survive at 16 ºC, as all larvae died at this temperature. However, with the increase of temperature, survival rate of the larvae increased, and they were able to complete their development at temperatures higher than 18 ºC. At this temperature, the rate of survival was very low (6%). It was generally found to be low at the temperatures below 25 ºC, but it increased to the range of 35-58% at temperatures above 25 ºC (table 2).

Table 2. Survival rate (%) of immature stages of *H. hebetor* reared on larvae of *G. mellonella* at different temperatures.

Temperature (ºC)	Survival rate (%)				
	Eggs	**Larvae**	**Pupae**	**Egg to female**	**Egg to male**
16	100a	0.0d	0.0e	0.0f	0.0d
18	100a	6cd	5de	1.5e	3.5c
20	98.75a	11.68c	11.68c	6.57d	5.11b
23	100a	22.16bc	20.54c	7.57d	12.97a
25	96.25a	25.96b	20.14c	9.03d	11.11a
28	98.5a	53.96a	42.8a	29.86a	12.84a
30	100a	35.48ba	28.39ba	15.48c	12.9a
32	98a	58.5a	48a	34.5a	13.5a
35	94.9a	44.5b	40.31ba	29.84a	1047a
38	98.5a	46b	35.5ba	24.5b	11a

Data within each column followed by the same letter are not statistically different by Duncan's Multiple Range Test (P = 0.05).

The relationship between temperature and the developmental rate of the parasitoid was well described by linear regression model ($R^2 = 0.89$ at egg stage and $R^2 = 0.95$ at adult stage) (fig. 1). The lower threshold temperature was obtained for eggs, and the other stages were very close to each other. The degree-day requirements were obtained for all growth stages. It was the lowest at the egg stage and the highest at the pupal stage. Temperature thresholds and degree-days for egg to adult in both sexes were very similar to each other (table 3).

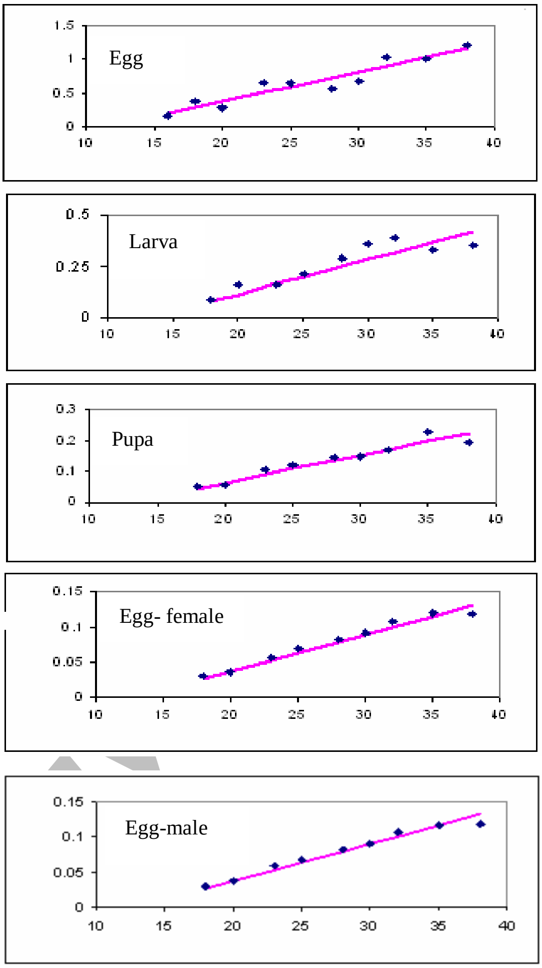

Figure 1. Linear regressions of developmental rate (1/day) for all stages of *H. hebetor* plotted against constant temperatures (ºC).

Discussion

Temperature is one of the most important factors affecting the population growth of arthropods. The relationship between temperature and the developmental rate of insects is linear over most of the range of exposing temperatures. Development ceases below a low-temperature threshold; above this the rate of development increases with temperature until an optimum is reached (Briere *et al.*, 1999). Our study has demonstrated the effects of temperature on the development, survivorship, longevity and developmental rate of

H. hebetor. As expected, the total development time and pupal survivorship decreased as temperature increased from 16 to 35 °C. The temperature range for development of *H. hebetor* lies between 18 and 38 ºC, with a mean development time lasting from 8.4 ± 0.069 to 32.7 ± 0.33 days for eggs to adult stage (females). These data suggest that temperatures between 28 and 38 ºC provide optimum conditions for rearing parasitoids in the shortest time. However, maximum production of parasitoids would need to consider overall mortality. Considering survival rate of larvae and pupae as an index, the mass production of the parasitoid would best be performed at rearing conditions between 25 and 32 ºC. The control and management of temperature in the insectarium is an important factor in the mass rearing and release of insects (Nakamori *et al*., 1975).

Table 3. Linear regressions of the developmental rate of different developmental stages of *H. hebetor* in relation to constant temperatures, calculation of threshold temperature and Degree-day requirements.

Growth Stages	Linear Regression models	R^2	P value	Threshold temperature (T_0) (ºC) - a/b	Degree-day (DD) 1/b
Egg	Y = -0.5045 + 0.044 X	0.89	0.0001	11.47	22.73
Larva	Y = -0.2266 + 0.0176 X	0.90	0.0001	12.88	56.82
Pupa	Y = -0.1199 + 0.0091X	0.92	0.0001	13.18	109.89
Egg to female adult	Y = -0.0699 + 0.0053 X	0.95	0.0001	13.19	188.68
Egg to male adult	Y = -0.0686 + 0.0053 X	0.95	0.0001	12.94	188.68

Our results are very similar to those obtained by Barfield *et al*. (1977) who studied the influence of temperature on the development of immature stages of *Bracon mellitor* Say, a braconid parasitoid of the boll weevil, *Anthonomus grandis* Boheman. According to their findings, the survival rate for eggs varied between 85% at 15.6 ºC to 100% at 32.2 ºC, and it was between 0 at 10 ºC and 81% at 26.7 ºC for egg-to-adult stage. Loni (1997) in a similar study on *Opius concolor* Szepligeti (Hym.: Braconidae) a parasitoid of *Bacterocera oleae* (Gemelin) and other tephritid flies found a survival rate of less than 1% (0.4-0.72) at 15 and 30 ºC and nearly similar values (31.84-36.16%) at 18, 20, 23 and 25 ºC. Miller (1996) also found a temperature-dependent development for *Meteorus communis* (Cresson) (Hym.: Braconidae) a parasitoid of the variegated cutworm and suggested an optimum conditions for rearing the parasitoid. Hussain & Jafar (1965) found that development time of immature stages of *H. hebetor* was between 7-12 days under field conditions, and the survival rate was particularly very low at the larval stage. Adashkevich & Saidova (1987) and Attaran (1996) found that the growth period of immature stages to be around 10 days at 30 ºC. The incubation period, larval development time and pupal period comprised 8-15%, 22-36% and 52-62% of the total egg to adult development time, respectively.

Common approaches to modelling insect development are based on deterministic models, such as linear degree-day models in which species-specific lower base thresholds are subtracted from daily average temperatures to yield a degree-day total (Wagner *et al*., 1984; Higley *et al*., 1986). Many research workers have used linear models to estimate degree-day requirements of insects. As Lopez *et al*. (2001) calculated the lower developmental threshold of *Sesamia nonagrioides* Léfévbre in the laboratory conditions using the linear model. Tobin *et al*. (2001) also used linear interpolation to estimate stage-specific base temperature thresholds and degree-day requirements of grape berry moth, *Endopiza viteana* (Clemens), under laboratory conditions. Kontodimas *et al*. (2004) in another study on the effect of temperature on the development of *Nephus includens* (Kirsch) and *N. bisignatus* (Boheman) (Col.: Coccinellidae) using the linear model, estimated the developmental zero (lower temperature threshold) as 10.9 and 9.4 ºC, and the thermal constant as 490.5 and 614.3 DD for *N. includens* and *N. bisignatus*, respectively. The development of *H. hebetor* at constant temperatures in the laboratory was described by linear model for all the developmental stages. Low threshold and thermal constant values were found to be very similar for both sexes (13.19 ºC, 188.68 DD for females and 12.94 ºC, 188.68 DD for males). Adashkevich & Saidova (1987) also reported the temperature threshold and thermal constant of *H. hebetor* as 12 ºC and 186.8 day-degrees for eggs to adult stages that are very close to our findings. Similar results were found by Miller (1996) for *Meteorus communis* and by Loni (1997) for *Opius concolor*.

Having more knowledge of insect and mite adaptations to climatic conditions plays a major role in pest management, specifically in helping to predict the timing of development, reproduction, and dormancy or migration (Nechols *et al*., 1999). The results in this study revealed that temperatures between 28 and 38 ºC provide a favourable condition for rearing *H. hebetor*. Regarding survival rate of larvae and pupae as an index, rearing conditions between 25 and 32 ºC would be the best for mass rearing of this parasitoid.

Acknowledgements

We are most grateful to the authorities of Iranian Research Institute of Plant Protection (IRIPP), Tehran, for their kind provision of the facilities needed for this research. Also, we dedicate our cordial thanks to Messrs Ali Akbar Hassani, Mahmoud Safari, and Mrs Marjan Bi Abi, the technicians in the Wheat Sunn Pest Research Department of IRIPP.

References

Adashkevich, B. P. & Saidova, E. Kh. (1987) Features of the development of *Habrobracon hebetor* (Hym.: Braconidae) during rearing in the laboratory. *Zoologicheskii Zhurnal* 66, 1509-1515.

AliNiazee, M. T. (1976) Thermal unit requirements for determining adult emergence of the western cherry fruitfly (Diptera: Tephritidae) in the Willamette valley of Oregon. *Environmental Entomology* 5, 397-402.

Amir-Maafi, M. & Chi, H. (2006) Demography of *Habrobracon hebetor* (Hymenoptera: Braconidae) on two pyralid hosts (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 99(1), 84-90.

Anonymous (2003) *Annual report of Plant Protection Organization*. 35 pp.

Attaran, M. R. (1996) Effect of laboratory hosts on the biological attributes of parasitoid wasp, *Habrobarcon hebetor* (Hymenoptera: Braconidae). M.Sc. thesis, College of Agriculture, Tabiat Modarres University, 83 pp. [In Persian with English summary].

Barfield, C. S., Sharp, P. J. H. & Bottrell, D. G. (1977) A temperature-driven developmental model for the parasite *Bracon mellitor* (Hym.: Braconidae). *Canandian Entomologist* 109, 1503-1514.

Briere, J. F, LeRoux, P. A. & Pierre, J. S. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology* 28(1), 22-29.

Campbell, A., Frazer, B. D., Gilbert, N., Gill, B., Gutierrez, A. P. & Mackauer, M. (1974) Temperature requirements of some aphids and their parasites. *Journal of Applied Ecology* 11, 431-438.

Cave, R. D. & Gaylor, M. J. (1988) Influence of temperature and humidity on development and survival of *Telenomus reynoldsi* parasitizing *Geocoris punctipes* eggs. *Annals of the Entomological Society of America* 81, 278-285.

Cheah, C. S. J. (1987) Temperature requirements of the chrysanthemum leafminer, *Chromatomyla syngenesiae*, and its ectoparasitoid, *Diglyphus isea*. *Entomophaga* 32, 357-365.

Curry, G. L., Feldman, R. M. & Sharpe, P. J. H. (1978) Foundations of stochastic development. *Journal of Theoretical Biology* 74, 397-410.

Davidson, J. (1944) On the relationship between temperature and rate of development of insects at constant temperature. *Journal of Animal Ecology* 13, 26-38.

Dowell, R. V. (1979) Synchrony and impact of *Amitus hesperidum* on its host, *Aleurocanthus woglumi* in Southern Florida. *Entomophaga* 24, 221-227.

Farahbakhsh, Gh. (1961). A checklist of major crops and agricultural products pests in Iran. Ministry of Agriculture.

Gilbert, D. W. (1988) Control of fecundity in *Pieris rapae* vs. comparisons between populations. *Journal of Animal Ecology* 57, 395-410.

Gilbert, D. W. & Raworth, D. A. (1996) Insects and temperature; a general theory. *Canadian Entomologist* 128, 1-13.

Higley, L. G., Pedigo, L. P. & Ostlie, K. R. (1986) DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach. *Environmental Entomology* 15, 999-1016.

Honek, A. (1999) Constraints on thermal requirements for insect development. *Entomological Sciences* 2, 615-621.

Howe, R. W. (1967) Temperature effects on embryonic development in insects. *Annual Review of Entomology* 12, 15-42.

Hussain, A. A. & Jafar, K. M. (1969) Biology of *Habrobracon hebetor* Say, with other mortality factors of its hosts in Iraq. *Bulletin de la Societe Entomologique d'Egypte*. 53, 227-233.

Jarosik, V., Honek, A. & Dixon, A. F. G. (2002) Developmental rate isomorphy in insects and mites. *American Naturalist* 160, 497-510.

Kontodimas, D. C., Eliopoulos, P. A., Stathas, G. J. & Economou, L. P. (2004) Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various nonlinear models using specific criteria. *Environmental Entomology* 33(1), 1-11.

Krugner, R., Daane, K. N., Lawson, A. B. & Yokota, G. Y. (2007) Temperature-development of *Macrocentrus iridescens* (Hymenoptera: Braconidae) as a parasitoid of the *obliquebanded leafroller* (Lepidoptera: Tortricidae): implications for field synchrony of parasitoid and host. *Biological control* 42, 110-118.

Liu, Y. H. & Tsai, J. H. (2002) Effect of temperature on development, survivorship, and fecundity of *Lysiphlebia mirzai* (Hymenoptera: Aphidiidae), a parasitoid of *Toxoptera citricida* (Homoptera: Aphididae). *Environmental Entomology* 31(2), 418-424.

Loni, A. D. (1997) Developmental rate of *Opius concolor* (Hym.: Braconidae) at various constant temperatures. *Georgia Entomological Society* 13, 227- 234.

Lopez, C., Sans, A., Asin, L. & Eizaguirre, M. (2001) Phenological model for *Sesamia nonagrioides* (Lepidoptera: Noctuidae). *Environmental Entomology* 30(1), 23-30.

Miller, J. C. (1996) Temperature-dependent development of *Meteorus communis* (Hymenoptera: Braconidae), a parasitoid of the variegated cutworm (Lepidoptera: Noctuidae). *Journal of Economic Entomology* 89 (4), 877-880.

Muniz, M. & Nombela, **G.** (2001) Differential variation in development of the B- and Q-Biotypes of *Bemisia tabaci* (Homoptera: Aleyrodidae) on sweet pepper at constant Temperatures. *Environmental Entomology* 30(4), 720-727.

Nakamori, H., Kakinohana, H. & Soemori, **H.** (1975) Mass rearing of the melon fly, *Dacus cucurbitae* Coquilett. I. Effect of rearing density on the yield and quantity of flies. *Journal of Okinawa Agriculture* 13, 27-32. [In Japanese].

Nechols, J. R., Tauber, M. J. Tauber, C. A. & Masaki, **S.** (1999) Adaptations to hazardous seasonal conditions: dormancy, migration, and polyphenism. pp. 159-200 in Huffaker, C. B. & Guttierez, A. P. (Eds) *Ecological entomology*. 2nd ed. 756 pp. Wiley, New York.

Obrycki, J. J. & Tauber, M. J. (1981) Phenology of three coccinellid species: thermal requirements for development. *Annals of the Entomological Society of America* 74, 31-36.

Quicke, D. L. J. & Van Achterberg, C. (1990) Phylogeny of the subfamilies of the family Braconidae (Hym.: Ichneumonidae). *Zoology Verhaulst* 158, 1-95.

Richards, A. G. (1957) Cumulative effects of optimum and suboptimum temperatures on insect development. pp. 57-65 in Johnson, F. H. (Ed.) *Influence of temperatures on biological systems*. American Physiological Society.

Tobin, P. C., Nagarkatti, S. & Saunders, **M. C.** (2001) Modelling development in grape berry moth (Lepidoptera: Tortricidae). *Environmental Entomology* 30(4), 692-699.

Uvarov, B. P. (1931) Insects and climate. *Transaction of Royal Entomological Society, London* 79, 1-247.

Wagner, T. L., Wu, H-I., Sharpe, P. J., Schoolfield, R. M. & Coulson, R. N. (1984) Modelling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America* 77, 208-225.

Worner, S. P. (1991) Use of models in applied entomology: the need for perspective. *Environmental Entomology* 20, 763-769.

Worner, S. P. (1992) Performance of phenological models under variable temperature regimes: consequences of the Kaufman or rate summation effect. *Environmental Entomology* 21, 689-699.

Received: 12 November 2007
Accepted: 25 February 2008