

Temperature-dependent development of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and its larval parasitoid, *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae): implications for species interactions

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Abstract

Habrobracon hebetor (Say) is a parasitoid of various Lepidoptera including *Helicoverpa armigera* (Hübner), a key pest of different crops and vegetables. The development of both *H. armigera* and *H. hebetor* were simultaneously evaluated against a wide range of constant temperatures (10, 15, 17.5, 20, 25, 27.5, 30, 35, 37.5 and 40 °C). *Helicoverpa armigera* completed its development from egg to adult within a temperature range of 17.5–37.5 °C and *H. hebetor* completed its life cycle from egg to adult within a temperature range of 15–40 °C. Based on the Ikemoto and Takai model the developmental threshold (T_o) and thermal constant (K) to complete the immature stages, of *H. armigera* were calculated as 11.6 °C and 513.6 DD, respectively, and 13 °C and 148 DD, respectively, for *H. hebetor*. Analytis/Briere-2 and Analytis/Briere-1 were adjudged the best non-linear models for prediction of phenology of *H. armigera* and *H. hebetor*, respectively and enabled estimation of the optimum (T_{opt}) and maximum temperature (T_{max}) for development with values of 34.8, 38.7, 36.3, and 43 °C for host and the parasitoid, respectively. Parasitisation by *H. hebetor* was maximal at 25 °C but occurred even at 40 °C. This study suggests although high temperature is limiting to insects, our estimates of the upper thermal limits for both species are higher than previously estimated. Some biological control of *H. armigera* by *H. hebetor* may persist in tropical areas, even with increasing temperatures due to climate change.

Keywords: biological control, cotton bollworm, developmental threshold, degree days, linear model, upper thermal limits

(Accepted 10 July 2017; First published online 24 August 2017)

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Introduction

Various biotic and abiotic factors affect the behaviour of pests and the efficiency of their biocontrol agents. Temperature is one prominent abiotic factor influencing

development (Visser & Both, 2005) and reproductive potential of insects (Mironidis & Savopoulou-Soultani, 2008) and subsequently their population dynamics (Logan *et al.*, 2006). An increase in temperature may contract or expand the distribution of a given pest (Powell & Logan, 2005) and its natural enemies (Furlong *et al.*, 2016).

The likely increase in temperature due to changing climate will have a great bearing on the effectiveness of natural enemies for pest management, which in turn will affect insect host-natural enemy associations, crop production and food security (Dhillon & Sharma, 2009) because both host and parasitoid may have different thermal curves (Hance *et al.*, 2007; Furlong & Zalucki, 2017). Our understanding of biological control and ability to manipulate the interaction is facilitated when the relationship between climate, predominately temperature and biocontrol agents and their hosts is known (Golizadeh *et al.*, 2008). Thermal requirements of insects have both ecological and practical utility (Damos & Savopoulou-Soultani, 2011). Thermal constants and developmental thresholds influence the success of biocontrol agents by affecting their activity and abundance (Furlong & Zalucki, 2017). Differences in lower developmental thresholds of insect predator and prey affect predator-prey dynamics (Dixon, 2006). In addition, time of appearance of natural enemies can be predicted using thermal constants (Malina & Praslicka, 2008) and thermal thresholds help to predict occurrence and abundance of biocontrol agents (Dhillon & Sharma, 2009). Developmental thresholds and thermal requirements can be used to select biocontrol agents that are adapted to conditions, which are suitable for their prey (Obrycki & Kring, 1998; Perdakis & Lykouressis, 2002) and to select suitable temperatures for mass rearing of insects (Torres *et al.*, 2002). Knowing the thermal requirements of an insect can aid interpretation of its present geographical distribution and in predicting its future distribution (Hance *et al.*, 2007).

Helicoverpa armigera, also known as the cotton bollworm, is one of the most important pests of cotton. *H. armigera* is found almost throughout the world (Europe, Africa, Asia and Australia), recently invaded South America and is likely to spread to North America (Kriticos *et al.*, 2015; Downes *et al.*, 2016). *Habrobracon hebetor* (Say) is an idiobiont, gregarious ecto-parasitoid that targets pyralid species (Brower & Press, 1990) as well as various other lepidopteran larvae (Chen *et al.*, 2013). It has potential as a biological control agent against *H. armigera* (Nikam & Pawar, 1993) in different parts of world (Imam *et al.*, 2007; Ashfaq *et al.*, 2011). Females first paralyse the host larvae and then lay 2–3 eggs on the larval surface. After 3–5 days, the eggs hatch and larvae start to feed on the paralysed host larva for approximately 10 days after which pupation occurs. Adults emerge from pupae after 8–9 days and start searching for new host larvae (Ode *et al.*, 1996).

Thermal effects on development of *H. armigera* have been studied in various parts of world, including Australia (Foley, 1981; Kay, 1981; Room, 1983), Japan (Jallow & Matsumura, 2001) and Greece (Mironidis & Savopoulou-Soultani, 2008). Forouzan *et al.* (2008) and Ahmad *et al.* (1985) studied development of *H. hebetor* in relation to temperature with *Galleria mellonella* L. and *Ephestia cautella* (Walker), respectively, as the hosts but did not cover a wider range of temperatures suitable for development of *H. hebetor*. Development and reproductive biology of insects may differ with geographical regions (Tsoukanas *et al.*, 2006). Therefore species thermal requirements should be tested with local populations. There are no reports on the effect of temperature on *H. hebetor* with *H.*

armigera as a host. Vingradova & Reznik (2015) concluded that using a wide range of constant temperatures is comparable with natural thermorhythms in relation to rate of development. Therefore, we establish the influence of temperature on *H. armigera* and its parasitoid, *H. hebetor* across a wide range of constant temperatures. Both host and parasitoid were sourced from Pakistan. We were interested in the thermal optima and high-temperature effects, as well as establishing the developmental threshold and degree days for each species.

Materials and Methods

Culturing of *H. armigera* and *H. hebetor*

Adult *H. armigera* collected from cotton fields near Faisalabad (Latitude, 31.4181N; Longitude, 73.0776E), (Punjab), Pakistan in light traps were placed in plastic jars (45 cm diameter and 30 cm depth) covered with muslin cloth. A 10% solution of honey in water was provided, on soaked cotton pads, to feed the adults. A piece of nappy liner was hung inside the jar in order to collect eggs. Larvae were reared on a semi-synthetic diet (Ahmad *et al.*, 1995) for up to four generations.

All developmental stages of the Greater Wax Moth, *G. mellonella* were collected from infested bee hives. Adults were kept in plastic jars 25 cm diameter and 30 cm deep, for mating and egg collection and larvae were reared on artificial diet (Khan *et al.*, 2011). Adults and larvae were incubated in a growth chamber, at optimum conditions of $30 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH (Khan *et al.*, 2011). Adults of *H. hebetor* were obtained from the parasitized larvae of *H. armigera* from cotton and tomato field, from Faisalabad, (Punjab), Pakistan. The adults were then reared, in the laboratory up to four generations, on larvae of *G. mellonella* to establish a colony, at $29 \pm 1^\circ\text{C}$ and $65 \pm 1\%$ RH, with 16:8 L:D hours, in glass vials of 5 cm diameter and 10 cm depth. Each female in a vial was offered a 4th–5th instar larva of the host along with 20% honey solution in water soaked in cotton swab. After 24 h, the female *H. hebetor* were moved to another vial containing a larva of *G. mellonella* and the parasitized larvae incubated as described above.

Temperature-dependent development and survival of immature stages of *H. armigera* and *H. hebetor*

Eggs of *H. armigera* (<24 h old) were placed in Petri dishes (6 cm in diameter) containing artificial diet and subjected to a range of constant temperatures, i.e. 10, 15, 17.5, 20, 25, 27.5, 30, 35, 37.5, 40 °C (all $\pm 1/2^\circ\text{C}$) with $65 \pm 1\%$ RH, with 16:8 L:D hours in controlled environmental chamber (GC-1000 DD, Usman Technical Services, Faisalabad, Punjab, Pakistan). A batch of 150–350 eggs of *H. armigera* was placed at 10–30 °C, while 400–550 eggs were used at 35, 37.5 and 40 °C. Hatching of eggs (and later larval development) was recorded daily at 10, 15, 20 and 25 °C and at twice a day for the higher temperatures (30, 35, 37.5 and 40 °C). Larvae were placed in individual Petri dishes (6 cm in diameter) to avoid cannibalism. Larval development was recorded until pupation and the duration of pupal development was observed.

Four-day-old mated female *H. hebetor* were transferred individually into glass vials ($10 \times 5 \text{ cm}^2$) each containing a 5th instar larva of *H. armigera* with its artificial diet. Fifth instar larvae of *H. armigera* are a suitable stage for parasitism by

H. hebetor (Saxena *et al.*, 2012). Wasp females were provided with 20% honey solution via cotton swabs. Egg laying was checked at 4 h intervals when larvae with eggs were transferred to a Petri dish (6 cm in diameter), and then subjected to constant temperatures range (10–40 °C). The duration of development of eggs of *H. hebetor* was recorded at 4 h intervals, while larval and pupal development was observed at 24 h intervals.

Temperature-dependent parasitism of *H. hebetor*

Pairs of 4 d old *H. hebetor* adults ($n = 30$ pairs per replicate) were each provided with ten 5th instar larvae at each constant temperatures from 10 to 40 °C. Larvae of *H. armigera*, along with artificial diet, were provided individually to each pair to avoid cannibalism in a glass vial (10 × 5 cm²) for a period of 48 h. Parasitoids were provided with 20% honey solution supplied by cotton swab, until all 10 larvae had been proffered (each pair took 20 days). The number of parasitized larvae was scored based on parasitoid pupal formation. This procedure was replicated three times, i.e. 90 pairs of parasitoids in total were trialled at each tested temperature to estimate parasitism.

Model fitting and analysis

The effect of different temperatures on developmental stages was analysed by One-way analysis of variance (ANOVA) using SPSS software and means were compared by Tukey's Honest Significant Difference (HSD) test at $P \leq 0.05$. The survival rate and parasitism were subjected to quadratic regression in order to show the relationship with temperature. The effect of temperature on insect development was established using a linear regression; viz. $Y = a + bT$, where Y is the developmental rate (1/time in stage) at each temperature T , a is the intercept, and b is the slope of the fitted line. The lower developmental threshold (T_0) and thermal constant (k) were calculated as: $T_0 = -a/b$ and $k = 1/b$ (Campbell *et al.*, 1974). The Ikemoto & Takai (2000) regression method, used to calculate DD and T_0 , fits $DT = k + T_0 \times D$, where D is the duration of development (in days), Biological parameters (T_0 and k) for both linear models were compared by the paired t -test.

Various non-linear models available in the literature to describe insect development with temperature; Pradhan–Taylor (Gaussian), Davidsons logistic, Logan-6, Logan-6/Lactin-2, Logan-6/Lactin 1, Logan-10, Hilbert and Logan, Analytis-1/Allahyari, Analytis-1, Analytis-3/Kontodimas, Analytis-3/Briere-1, Analytis-3/Briere-2, Janisch/Analytis, Janisch/Rochat, Polynomial (cubic), Shi-1, Shi-2 and Wang model; were applied to development data across the range of temperatures used for both *H. armigera* and *H. hebetor*. These models are frequently used to depict the relationship between temperature and arthropod developmental rates (e.g. Zahiri *et al.*, 2010; Shi *et al.*, 2011; Bahar *et al.*, 2014). Calculations were made using MATLAB R 2016b.

Model evaluation

The best-fit model was assessed based on the coefficient of nonlinear regression (for non-linear models; R^2), sum of squares error (SSE) and biological criteria. High R^2 and lower SSE are the usual criteria for best-fit models (Walgama & Zalucki, 2006). Because non-linear models differ in the number of parameters that need to be estimated an

addition criteria is often applied to discriminate amongst the models. We employed Akaike information criterion (AIC) to appraise goodness of fit of non-linear models (Akaike, 1974). AIC is defined as: $AIC = 2k - 2\ln(L)$, where k is the number of estimated parameters for the model, L is the maximum value of the likelihood function for the model and \ln is the natural log. The best-fit model would have lower value of AIC.

Lastly the best-fitting non-linear models were assessed on biological grounds as parameters by comparing estimates of T_0 , T_{opt} and T_{max} : the low-temperature threshold, optimal temperature and high-temperature threshold, respectively with experimental data. Non-linear models can give nonsensical values for these due to the form of the function at temperature extremes and extrapolation errors; such model could not consider as best fit model, even though they may have high R^2 values.

Results

Temperature influence on *H. armigera* and *H. hebetor*

Development

No stage of *H. armigera* could complete development at 40 °C. Below 40 °C temperature had a significant effect on the developmental period of eggs ($F = 3389$, $DF = 1, 5$ and $P < 0.001$), larvae ($F = 2671$, $DF = 1, 4$ and $P < 0.001$) and pupae ($F = 556$, $DF = 1, 3$ and $P < 0.001$) (fig. 1). Eggs of *H. armigera* completed their development 2.2 days at 35 °C and took longer at temperatures below and above 35 °C. Larvae of *H. armigera* were not able to complete their development at 10 °C but, as with the eggs, the development period decreased with increasing temperatures; 70 days at 15 °C to 11 days at 35 °C. Pupae of *H. armigera* could not complete development at 10 and 15 °C, but the developmental period decreased from 22 days at 20 °C to 9 days at 35 °C. Developmental period of *H. armigera* increased for all immature stages at 37.5 °C (table 1). Temperature significantly ($P < 0.001$) affected the developmental period of eggs ($F = 387$, $DF = 1, 6$), larvae ($F = 1076$, $DF = 1, 5$) and pupae ($F = 439$, $DF = 1, 4$), of *H. hebetor* (fig. 1). As expected the developmental period of each immature stage of *H. hebetor* decreased with an increase in temperature except at 37.5 and 40 °C. Unlike *H. armigera*, eggs of the parasitoid completed their development at 40 °C and pupae developed at 15 °C; as with *H. armigera*, larvae of *H. hebetor* could not survive at 10 °C.

Survival

The highest survival of *H. armigera* was observed at 25 °C (fig. 2). Based on the fitted curves survival was optimal at 23.2 °C (61%), 24.3 °C (87%) and 25.1 °C (77%) for eggs, larvae, pupae of *H. armigera*, respectively (fig. 2). Larvae of *H. armigera* showed the highest survival and were less affected by temperature above and below the optimum than eggs or pupae. As was observed with its *H. armigera* host, survival of all stages of *H. hebetor* was greatest at 25 °C (fig. 2) and then tailed off at either higher or lower temperatures. Based on the fitted curves survival rate of *H. hebetor* was 53% at 25.2 °C, 81% at 25.8 °C and 76% at 26 °C for eggs, larvae and pupae, respectively (fig. 2).

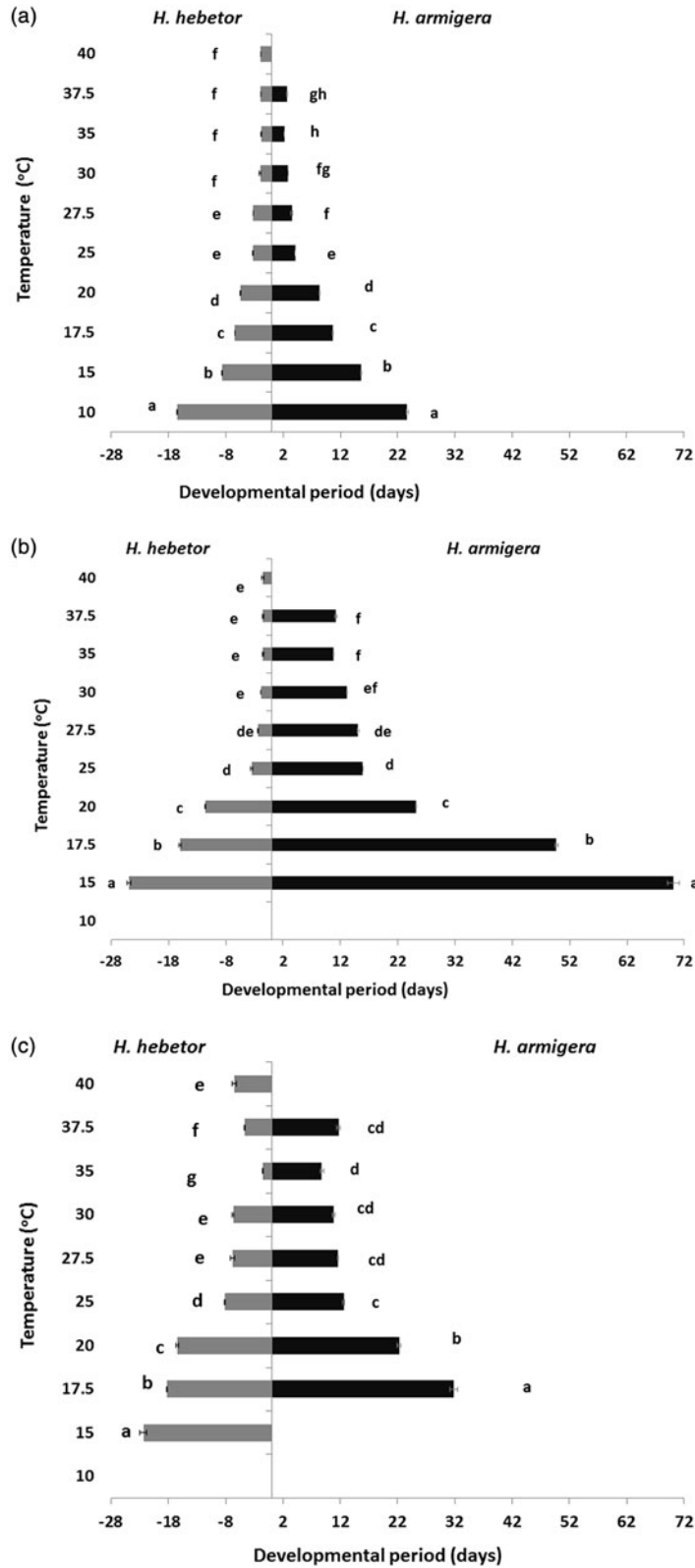


Fig. 1. Development time (days \pm SE) of immature stages of *H. hebetor* and *H. armigera* (eggs, larvae and pupae) at ten constant temperatures from 10 to 40 °C (see the text for details).

Table 1. Linear regression models (ordinary and Ikemoto) parameters and R^2 values for temperature dependent development of immature stages (eggs, larvae, pupae and combined immature stages) of *H. armigera* and *H. hebetor*.

Insect	Stage	Linear models							
		Ordinary model				Ikemoto model			
		Equation	R^2	T	K	Equation	R^2	T	K
<i>H. armigera</i>	Eggs	$-0.18 + 0.01T$	0.95	10.6	57.8	$76.50 + 8.15D$	0.88	8.1	76.5
	Larvae	$-0.04 + 0.00T$	0.98	11.1	247.7	$243.52 + 11.75D$	0.99	11.7	243.5
	Pupae	$-0.04 + 0.004T$	0.97	9.9	213	$224.14 + 10.40D$	0.79	10.4	224.1
	Total immature stages	$-0.02 + 0.001T$	0.97	11.0	508.6	$513.68 + 11.61D$	0.93	11.6	513.6
<i>H. hebetor</i>	Eggs	$-0.19 + 0.02T$	0.91	9.5	47.5	$60.10 + 6.95D$	0.91	7.0	60.1
	Larvae	$-0.55 + 0.03T$	0.91	15.7	28.3	$37.77 + 14.30D$	0.98	14.3	37.8
	Pupae	$-0.44 + 0.02T$	0.56	17.2	38.8	$84.30 + 12.93D$	0.89	12.9	84.3
	Total immature stages	$-0.13 + 0.008T$	0.82	15.0	111.1	$147.19 + 13.21D$	0.96	13.2	147.1

T_o , developmental threshold; K (DD), thermal constant (degree-day), *(egg to adult emergence).

Relationship between development rate and temperature

Linear regression models for each developmental stage were used to calculate threshold temperatures and degree days to complete development (table 1). The Ikemoto and Takai model and ordinary regression model were not statistically different for developmental threshold ($t = 0.261$, $P > 0.05$) and k ($t = -1.581$, $P > 0.05$) in case of *H. armigera*. Using the Ikemoto and Takai model the pattern of T_o for *H. armigera* was larva (11.7 °C) > pupa (10.4 °C) > Egg (8.1 °C).

In case of *H. hebetor* the two linear models differed in their estimate of T_o ($t = 4.029$, $P < 0.05$). Larvae of *H. hebetor* showed a higher threshold (14.3 °C) than pupae (12.9 °C) or eggs (7 °C) based on the Ikemoto and Takai model (table 1). Most non-linear models could be fitted to all developmental stages except Shi-2 in case of *H. armigera*. This model could only be fitted to eggs along with larval period as parameter estimates failed to converge in these cases. The selected models for the entire immature period differed in their ability to estimate pivotal temperatures (T_{min} , T_{opt} and T_{max}) for *H. armigera* (table 2, fig. 3). Analytis-3/Briere-2 model was adjudged the best model for entire developmental period of *H. armigera* due to its biological significance (see the Discussion). The estimated values for T_o , T_{opt} and T_{max} are 8.5, 34.8 and 38.7 °C, respectively. Using the best-fit models of *H. hebetor* (table 2, fig. 3) the calculated values of T_o , T_{opt} and T_{max} are 13.3, 37.2 and 40.5 °C, respectively, based on the biological significance (see the section Discussion).

Parasitism

The level of parasitism varied with temperature (fig. 4) with the highest level (99.8%) being observed at 25 °C. This reduced to 52% at 15 °C and 13% at 40 °C.

Discussion

As expected immature life stages of both *H. armigera* and *H. hebetor* completed their development in shorter times at high temperatures up to an optimum temperature. A similar pattern of developmental period against temperature was previously recorded for *H. armigera* (Jallow & Matsumura, 2001; Bartekova & Praslicka, 2006) and *H. hebetor* (Engroff & Watson, 1975; Thanavendan & Jeyarani, 2010). However, developmental period in our study is shorter than observed

in other studies on *H. armigera*, which were carried out on a population from Japan when reared on tomato (Jallow & Matsumura, 2001), on one from Slovakia reared on corn seeds (Bartekova & Praslicka, 2006) but higher values of developmental period than a population from Greece reared on artificial diet (Mironidis & Savopoulou-Soultani, 2008). Developmental thresholds of *H. armigera* recorded in our study (11–12 °C) were in agreement with other studies (Jallow & Matsumura, 2001; Mironidis & Savopoulou-Soultani, 2008). However, Bartekova & Praslicka (2006) and Foley (1981) determined a higher developmental threshold for eggs (14.8 °C), and non-diapausing pupae (14.8 °C). The life history traits may differ among the population of different geographical regions (Tsoukanas *et al.*, 2006), rearing techniques and diet.

The developmental period of *H. hebetor* observed in the present study differed from that of Forouzan *et al.* (2008) who observed higher values of developmental period for *H. hebetor* on *G. mellonella*. In contrast, Ahmad *et al.* (1985) recorded a slightly lower developmental duration of *H. hebetor* on *E. cautella*. In the present study, *H. hebetor* were unable to survive and complete development only at 10 °C. In contrast, survival rate of *H. hebetor* was zero at 16 °C for larvae and pupae when reared on *G. mellonella* in Iran (Forouzan *et al.*, 2008). These differences in aspects of life history traits may be due to different strain of *H. hebetor*, rearing host and/or geographical origin. The lower developmental threshold (15 °C) for *H. hebetor* calculated in our study is higher than that calculated (13 °C) by Forouzan *et al.* (2008) who used a different host (*G. mellonella*). Variation in lower developmental threshold of insect predators and prey plays an important role in predator and prey dynamics (Dixon, 2006).

In this study, *H. armigera* completed its development within a narrower range of temperature (17.5–37.5 °C) than its parasitoid (15–40 °C), which contrasts to normal paradigm that parasitoids have generally narrow thermal tolerance than its host (Messenger & Bosch, 1971). Parasitoids with higher tolerance than its host may go extinct locally due to absence of its host (Bahar *et al.*, 2014). As *H. hebetor* is a generalist parasitoid, having a broad host range within the Lepidoptera, there is less chance of extinction of *H. hebetor* with climatic warming. The developmental periods for *H. hebetor* were shorter than for *H. armigera* over all temperatures. A shorter developmental period for the natural

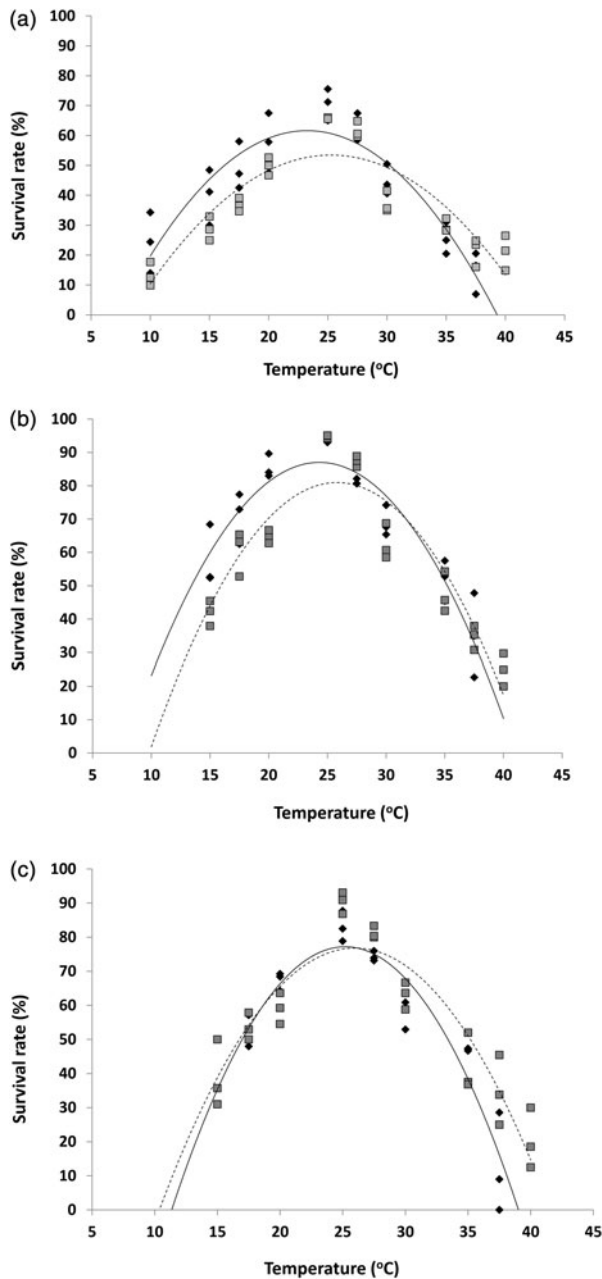


Fig. 2. Survival rate (%) of (a) eggs, (b) larvae, (c) pupae of *H. armigera* (●) and *H. hebetor* (■) at ten constant temperatures from 10 to 40 °C. Quadratic lines for *H. armigera* (solid lines) and *H. hebetor* (dotted lines) (a) Eggs: *H. armigera*, $Y = -0.2389x^2 + 11.107x - 67.456$, $R^2 = 0.82$ and *H. hebetor*, $Y = -0.1845x^2 + 9.3246x - 64.355$, $R^2 = 0.77$ (b) Larvae: *H. armigera*, $Y = -0.3115x^2 + 15.148x - 97.14$, $R^2 = 0.86$ and *H. hebetor*, $Y = -0.3162x^2 + 16.324x - 129.73$, $R^2 = 0.85$, and (c) Pupae: *H. armigera*, $Y = -0.4032x^2 + 20.311x - 178.61$, $R^2 = 0.88$ and *H. hebetor*, $Y = -0.3156x^2 + 16.394x - 136.05$, $R^2 = 0.83$.

enemy is helpful for successful biological control programs (Snyder & Ives, 2003) as there would be more generations compared with the host. Higher temperatures (>35 °C) are lethal to all stages of *H. armigera* (this study) as has been

found by others (Bashi & Tunc, 2008; Tran *et al.*, 2012). We found that *H. hebetor* completed its development at higher temperatures as compared with *H. armigera*. This finding suggests that *H. hebetor* can be used to control cotton boll-worm even in tropical areas. Low survival rates of *H. hebetor* at high temperatures (>37 °C) may be due to increased defence reaction such production of prophenoloxidase (PPOs) by the hosts (Spanoudis & Andreadis, 2012). Larvae of both *H. armigera* and *H. hebetor* were comparatively more heat tolerant than pupae or eggs. A possible explanation of this difference is production of more heat-shock proteins (Hsps) in the larval stage than at other immature stages (Sinha & Sanyal, 2013).

To overcome the pitfall of linear models, we evaluated the appropriateness of non-linear models based on how well they described the data (AIC ranking) and the estimated biological parameters (T_o , T_{opt} , T_{max}) (see the section Materials and Methods). Five models were selected based on AIC ranking for *H. armigera*: Wang, Shi-1, Logan-6/Lactin-2, Analytis-3/Briere-2, and Analytis-3/Briere-1. All provided adequate description of the data set (fig. 3). Estimates of key biological parameters were compared (table 2). Even though the Wang model provided reasonable estimates of T_{max} and T_{opt} ; 37.8 and 36.8 °C, respectively; the value of T_o (13.93 °C) appears to be too high (see linear models) and the model had more fitted parameters (6). The best fit must meet criteria of parsimony and fewer parameters with goodness of fit and biological significance (Walgama & Zalucki, 2006). The remaining four models (Shi-1, Logan-6/Lactin-2, Analytis-3/Briere-2, and Analytis-3/Briere-1) selected on AIC gave similar estimated values for biological parameters (table 3). We favoured the Analytis-3/Briere-2 model because it gave a T_{max} (38.7 °C) very similar to experimental result and had fewer fitted parameters.

The non-linear models for *H. hebetor* presented an interesting problem. Based on AIC criteria the top five models were Janisch/Rochat, Janisch/Analytis, Logan-10, Analytis-1/Allahyari and Pradhan-Taylor (Gaussian), but each gave unrealistic values for T_{max} (over 50 °C) or T_o (less than zero), which did not accord with experimental observations. We chose to look more closely at the next best fitting models: Polynomial (cubic), Hilbert and Logan, Analytis-3/Briere-2, Logan-6/Lactin-2 and Analytis-3/Briere-1 on the basis of AIC. We rejected the Polynomial (cubic) model as it cannot be used to calculate T_o . Hilbert and Logan model calculated appropriate T_{opt} , unrealistic T_{min} and slightly higher T_{max} than the remaining models (table 3). We did not consider this model further due to the higher number of parameters that need to be estimated (5). Failure of Analytis-3/Briere-2 model to be best fit for *H. hebetor* was due to unrealistic T_{opt} and T_{max} . Of the remaining models Analytis-1/Briere-1 was adjudged best as it required only three fitted parameters and gave appropriate biological parameters (T_{opt} and T_{max}). Using an appropriate biofix the first emergence of *H. hebetor* adults can be predicted using both linear and non-linear models.

Our data indicate that *H. hebetor* has the potential to be used as a biological control agent for *H. armigera* over a wide range of temperatures (fig. 4). The effect of temperature on life history traits for the two insects are very similar e.g. reductions in the development time of the host stages at higher temperatures are mirrored by equivalent reductions in the parasitoid. However, *H. hebetor* does better than *H. armigera* at higher temperatures. Higher

Table 2. Parameter estimates ± SE for selected non-linear models fitted (AIC-based ranking and biological significance) to describe the development rate of entire immature stages of *H. armigera* and *H. hebetor*. Estimated T_{min} , T_{opt} and T_{max} are also provided.

Model		Total immature stages	
Name	Parameters	<i>H. armigera</i>	<i>H. hebetor</i>
Logan-6/Lactin-2	P	$0.002 \pm 9.78 \times 10^{-5}$	0.007 ± 0.00
	T_{max}	46.269 ± 1.98	45.666 ± 5.33
	Δ	2.098 ± 0.5	2.045 ± 2.03
	λ	-1.025 ± 0.00	-1.107 ± 0.03
	T_{min}^*	12.1	14.5
	T_{opt}^*	34.8	36.8
	T_{max}^*	40.2	42.0
Analytis-3/Briere-1	A	$2.017 \times 10^{-5} \pm 1.40 \times 10^{-6}$	$7.8 \times 10^{-5} \pm 1.72 \times 10^{-5}$
	T_b	10.852 ± 0.82	14.55 ± 2.12
	TL	41.452 ± 0.46	43.079 ± 1.58
	T_{min}^*	11.2	14.8
	T_{opt}^*	34.5	36.3
	T_{max}^*	41.2	43.0
	Analytis-3/Briere-2	a	$3.442 \times 10^{-5} \pm 3.76 \times 10^{-6}$
T_b		8.205 ± 1.75	13.081 ± 3.69
TL		38.657 ± 0.65	40.497 ± 1.21
n		3.910 ± 1.05	4.345 ± 3.74
T_{min}^*		8.5	13.3
T_{opt}^*		34.8	37.1
T_{max}^*		38.7	40.4
Shi-I	M	0.002 ± 0.00	**
	T_{min}	12.001 ± 0.56	
	T_{max}	40.175 ± 0.63	
	K_2	0.458 ± 0.12	
	T_{min}^*	12.1	
	T_{opt}^*	34.9	
	T_{max}^*	40.2	
Wang	M	0.509 ± 8.00	**
	K_1	0.012 ± 0.20	
	T_0	13.769 ± 1.1	
	K_2	4.852 ± 0.00	
	T_m	37.848 ± 0.03	
	C	-0.023 ± 0.12	
	T_{min}^*	13.9	
	T_{opt}^*	36.8	
	T_{max}^*	37.8	
	Ψ	**	6.472 ± 22.94
Hilbert and Logan	T_b		9.061 ± 13.46
	D		$143.920 \pm 2.55 \times 10^5$
	T_m		36.768 ± 15.75
	Δ		3.277 ± 8.47
	T_{min}^*		9.3
	T_{opt}^*		36.4
	T_{max}^*		42.3
Polynomial (cubic)	a_0	**	$-5.3 \times 10^{-5} \pm 1.95 \times 10^{-5}$
	a_1		0.004 ± 0.00
	a_2		-0.101 ± 0.04
	a_3		0.761 ± 0.35
	T_{min}^*		Nil
	T_{opt}^*		35.5
	T_{max}^*		44.9

*Values obtained mathematically using Microsoft excel. **Not selected based on AIC and biological significance.

thermal tolerance of *H. hebetor* indicates that this parasitoid has features of an effective biocontrol agent both in cooler areas but also in warmer areas. It may coincide with the changing distribution of *H. armigera* in climate warming scenarios due to its high thermal tolerance. We directly tested the efficiency of parasitism at various temperatures and found that although the level dropped at the higher temperatures *H. hebetor* was still able to

parasitize *H. armigera* in laboratory assays at 40 °C and complete development. Thermal tolerance and parasitism indicate the potential of *H. hebetor* as an effective biological control agent to control *H. armigera*. Further studies are needed to explore the relationship of temperature with *H. hebetor* and its pest, *H. armigera* under fluctuating temperatures/natural conditions, as well as the effects of host plant and humidity.

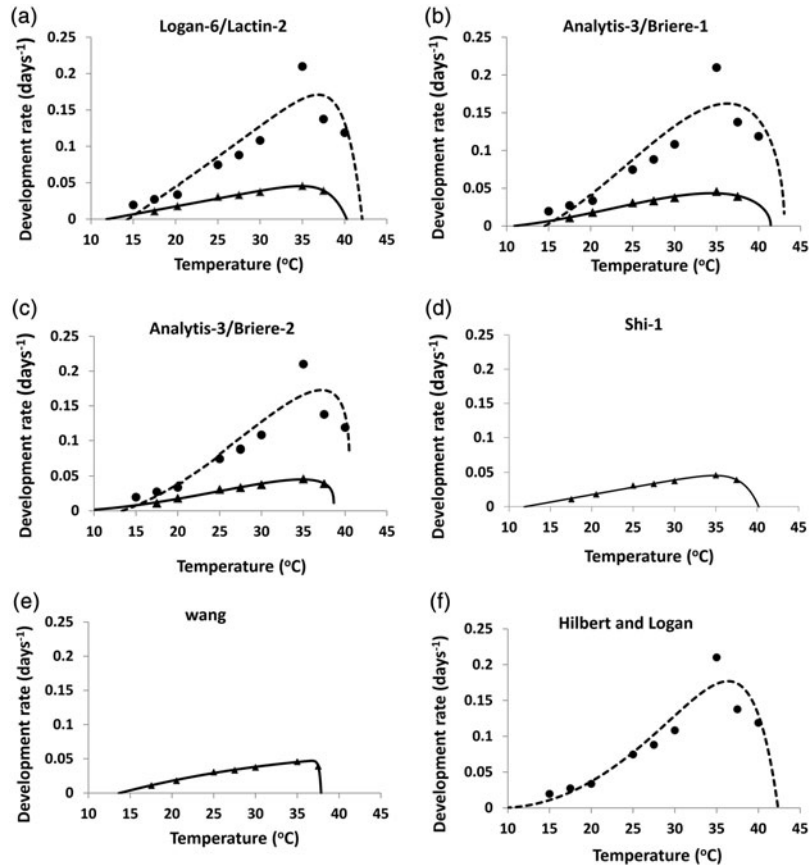


Fig. 3. Development rate for whole immature stages and best fit models for *H. armigera* and *H. hebetor*. Observed data (triangles) and fitted non-linear models (solid lines) of *H. armigera* and Observed data (dots) and fitted non-linear models (dotted lines) of *H. hebetor* (see table 2 for detail).

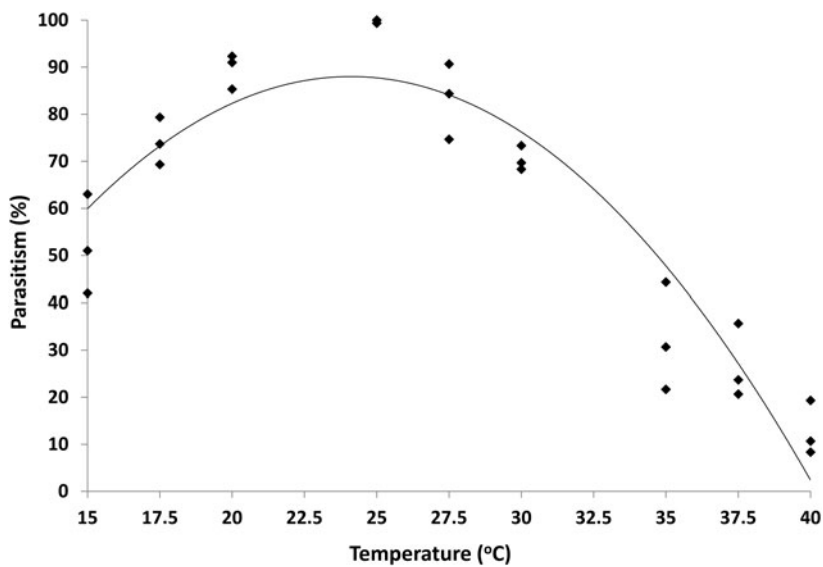


Fig. 4. Percentage of successful parasitism (Y) by *H. hebetor* of *H. armigera* late instar larvae at constant temperatures. Fitted line: $Y = -0.3388x^2 + 16.334x - 108.84$, $R^2 = 0.88$.

Acknowledgements

The authors are thankful to Higher Education Commission, Pakistan to sponsor this research, Yaghub Fathipour, Department of Entomology, Faculty of Agriculture, Tarbiat Modares University, Tehran, Iran, Dr M. Ashfaq and Dr Jalal Arif from University of Agriculture Faisalabad, Pakistan for helping out in different capacities and two anonymous referees for comments on early versions of the manuscript.

Disclosure

The authors have no potential conflicts of interests to disclose.

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