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Temperature-dependent development rates of *Bracon vulgaris*, a parasitoid of boll weevil

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Abstract The duration of development of *Bracon vulgaris* Ashmead, parasitoid of the boll weevil *Anthonomus grandis* Boheman, was determined at nine constant temperatures between 18°C and 38°C. Nonlinear regression analysis was used to test the fit of temperature-dependent development rates to the Sharpe and DeMichele and Lactin et al. models. At the highest tested temperature (38°C) all the parasitoid eggs died before hatching and no evidence of development was observed. The high values of R^2 for the models of Sharpe and DeMichele (0.8432 to 0.9834), and Lactin et al. (0.9071 to 0.9795) indicated that these models are suitable to estimate the development rate of *B. vulgaris* as a function of temperature. *B. vulgaris* showed tolerance to high temperature which is represented by the high value of H_H (change in enthalpy associated with high-temperature inactivation of the enzyme) for the prepupa stage of this insect obtained with the Sharpe and DeMichele model. According to that model, *B. vulgaris* exhibits thermal stress at 35.7°C, which indicates that maximum thermal stress estimated by this model was close to the real one.

Keywords *Anthonomus grandis* · Nonlinear models · Sharpe and DeMichele model · Lactin et al. model

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Introduction

The ectoparasitoid *Bracon vulgaris* Ashmead is a major natural enemy which may be employed for reduction of boll weevil (*Anthonomus grandis* Boheman) populations in the cotton agro-ecosystems in the Brazilian northeast (Ramalho et al. 1993).

The relationship between development rate and temperature represents an important ecological tool to model population dynamics of insects (Howe 1967; Uvarov 1931; Wanderley et al. 2007). Several authors (e.g. Lactin et al. 1995; Schoolfield et al. 1981) formulated mathematical models to describe this relationship. The knowledge of such relationships is important to determine seasonal occurrences of insect populations in integrated pest management strategies (Marco et al. 1997).

Modeling the effect of *B. vulgaris* on the boll weevil's population dynamics is an important step in

implementing a biological control program against this pest, applying augmentation tactics. Determining development rates as a function of temperature is required for the development of a simulation model of parasitoid–host population dynamics under changing temperatures. Because temperatures normally exceed 35°C at least during part of summer days in Brazil, high-temperature inhibition of *B. vulgaris* became a concern. For this reason, temperature-dependent development rates were fit to two nonlinear models, namely, the Sharpe and DeMichele model (Sharpe and Hu 1980) and one variant (Lactin et al. 1995) of the model of Logan et al. (1976). Such models provide estimates of temperatures at which inhibition occurs. This study is the first step in the construction of a detailed population simulation model to predict field phenology and density of *B. vulgaris* to help optimize the use of this biological control agent in controlling boll weevil at various locations throughout northeastern Brazil.

Materials and methods

The research was carried out at the Biological Control Unit (BCU) of the National Center for Cotton Plant Research (Embrapa Cotton), Campina Grande, Paraíba State, Brazil. *B. vulgaris* specimens were obtained from third generation colonies of the BCU/Embrapa Cotton. Third instar *A. grandis* larvae were collected in upland cotton bolls (*Gossypium hirsutum* L. race *latifolium* Hutch.) CNPA Precoce cultivar planted at Embrapa Cotton Research and used as a rearing host. The research was carried out in environmental chambers at constant temperatures (18°C, 20°C, 23°C, 25°C, 28°C, 30°C, 33°C, 35°C, and 38°C), 70±10% r.h. and 14L/10D photoperiod.

Cotton bolls attacked by *A. grandis* were collected and taken to the laboratory and dissected. Third instar larvae of this insect were removed and disinfected with 10% sodium hypochlorite for 10 min, after which they were transferred to the previously molded parafilm pads. These parafilm pads with larvae were taken to the rearing box and exposed to gravid females of *B. vulgaris* for 6 h. The parasitized larvae were placed individually on ELISA plastic plate wells, with one parasitoid egg fixed in the dorsal region of each boll weevil larva. Fifty *B. vulgaris* eggs were used for each constant temperature. The number of larval instars of *B. vulgaris* was determined by marking the cuticle of the parasitoid larvae with Day-Glow powder. The change of instar was confirmed by two criteria: the absence of the powder mark on the cuticle and the presence of the marked parasitoid exuviae. The immature forms of this parasitoid were observed every 6 h with a stereoscopic microscope. The duration of egg incubation, larval instars, prepupa and pupal stages of *B. vulgaris* was registered.

Mean development rate of *B. vulgaris* at different temperatures was estimated with the formula:

$$D_{\mathrm{M}} = 1.0/\exp\left[\left(\sum_{i=1}^{n}\ln(d_i)\right)\Big/ n\right] \quad (1)$$

where D_{M} is the daily mean rate of development at temperature T (°C); d_{i}, individual observations of development time in days; and n is the sample size. This method is recommended by Logan et al. (1976) to account for linearity in the transformation from development time to development rate.

Development rate is the reciprocal of development time in days and it is represented by values from 0 to 1. These rates are used in development models where data are added each day. The development of an organism is completed when the sum of their daily rate of development reaches 1 (Cury and Feldman 1987). Therefore, the integral of the function of development rate along time as the methods of Sharpe and DeMichele (1977) and Lactin et al. (1995) can be used to simulate the development of an organism submitted to changes in temperature. For this reason, descriptive nonlinear procedures have been used to analyze the relationship between development rate of *B. vulgaris* and temperature as described.

The Sharpe and DeMichele (1977) biophysical model, modified by Schoolfield et al. (1981), is represented by the following equation:

$$R(T) = \frac{\mathrm{RHO}_{25}\left(\frac{T}{298.15}\right)\exp\left[\left(\frac{H_A}{\mathrm{Rq}}\right)\left(\frac{1}{298.15}-\frac{1}{T}\right)\right]}{1+\exp\left[\left(\frac{H_{\mathrm{L}}}{\mathrm{Rq}}\right)\left(\frac{1}{T_{\mathrm{L}}}-\frac{1}{T}\right)\right]+\exp\left[\left(\frac{H_{\mathrm{H}}}{\mathrm{Rq}}\right)\left(\frac{1}{T_{\mathrm{H}}}-\frac{1}{T}\right)\right]} \quad (2)$$

where $R(T)$ is the mean development rate (equivalent to D_{M}) at temperature T (K); the universal gas

constant (1.987 cal K^{-1} mol^{-1}), RHO_{25}; the development rate at 25°C (298.15°K), assuming no enzyme inactivation; H_A, the enthalpy of activation of the reaction that is catalyzed by a rate-controlling enzyme; T_L Kelvin temperature at which the rate-controlling enzyme is half active and half low-temperature inactive; H_L, the change in the enthalpy associated with low temperature inactivation of the enzyme; T_H, Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive; and H_H, the change in the enthalpy associated with high-temperature inactivation of the enzyme. The parameters RHO_{25}, H_A, T_H and H_H were estimated by Marquardt's method using PROC NLIN (SAS Institute 2004) with the procedure adopted by Wagner et al. (1984).

The numerator of the second equation explains the dependent development rates of the temperature in the absence of inactivation at low or high temperatures, while first and second exponential equations in the denominator explain, respectively, the inhibition at low and high temperatures (Wagner et al. 1984). Wagner et al. (1984) developed a method to determine if data are adjusted by a model constituted by six, four or two parameters. This method tests the nonlinearity of data to extreme temperatures (low and high), which would indicate inhibition at extreme temperatures. The model is constituted by six parameters and it is better adjusted to the data if neither extreme temperature has a significant effect on the inhibition**.** When high temperatures have no effect on inhibition, the parameters T_H and H_H will assume constant values of 10^3 and 10^8, respectively. If low temperature does not have a significant effect on the inhibition, the parameters T_L and H_L will receive constant values of 100 and -10^8, respectively. Therefore, in both cases, a four-parameter model would fit the data better. When low and high temperatures have no effect on inhibition, the model with two parameters will better fit the data; then, the four parameters T_H, H_H, T_L and H_L will receive constant values of 10^3, 10^8, 100, and -10^8, respectively.

The values of the parameters T_H and T_L were estimated for boll weevil females using the published data of Bacheler et al. (1975). Similarly, data published by Barfield et al. (1977) on development rates of *B. mellitor* females were used to estimate T_H and T_L.

The model of Lactin et al. (1995) resulted from the modification of the nonlinear model of Logan et al. (1976):

$$R(T) = e^{\rho T} - e\left[\rho T_L - \left(\frac{T_L - T}{\Delta_T}\right)\right] + \lambda \qquad (3)$$

where $R(T)$ is the mean development rate at temperature T (°C); T_L, lethal temperature (°C); ρ, rate of increase at optimal temperature; Δ_T, difference between lethal and optimal temperature of development; and λ, the parameter that makes the curve intercept the x-axis, allowing to estimate development threshold. The parameter λ is the value of the rate R (T_L) (i.e., when $T = T_L$) and allows the curve to intersect the abscissa at suboptimal temperatures, permitting estimation of the base temperature by allowing $R(T)=0$ to be solved for particular parameter values. The upper threshold (Tupper) is the value of T for which $R(T)$ is maximum (i.e., the first derivative, $R'(T)$, is equated to zero and solved for T), then $R'(T) = dR(T)/dT = \rho \times \exp(\rho^T) - (1/\Delta_T) \times \exp[\rho \times T_L - (T_L - T)/\Delta_T]$ which evaluated at $T=0$ gives the initial rate, equivalent to parameter b of the x-intercept method. The value of T for which $R'(T)=0$ is then $\text{Tupper} = [\Delta_T \times \log_e(\Delta_T \times \rho)/(1 - \Delta_T \times \rho)] + T_L$, which is equivalent to the expression given by Logan et al. (1976). Parameters T_L, ρ, Δ_T, and λ were estimated by Marquardt's method using PROC NLIN (SAS 2004).

The coefficient of determination (R^2) of nonlinear models cannot be calculated as in linear models [$R^2 = 1 - (\text{SSR/TSS})$], mainly because most nonlinear models do not contain an identifiable intercept term. As a consequence, the SAS software uses the uncorrelated sum of squares as total sum of squares (Freund and Littell 1986). The R^2 of these models were calculated as $R^2 = 1\left(S^2_{\text{YERR}}/S^2_{\text{D}}\right)$, where $S^2{}_{\text{YERR}}$ is the variance of the model residuals and $S^2{}_{\text{D}}$ is the variance of the observed means of development rates. This method was used by Wagner et al. (1984) to obtain R^2 in their SAS program.

Results and discussion

Temperature and development The duration of the egg [$F(1,395)=2.42$; $P=0.178$], larva [$F(1,371)=1.02$; $P=0.210$], prepupa [$F(1,258)=1.87$; $P=0.322$]

Table 1 Development time (days; means±SE) of *Bracon vulgaris* fed on *Anthonomus grandis* larvae at temperatures from 18°C to 35°C, 70±10% r.h. and photoperiod of 14L/10D

Life stage	Temperature (°C)							
	18	20	23	25	28	30	33	35
Egg[a]	1.90±0.02 (50)[b]	1.34±0.01 (50)	1.21±0.03 (50)	0.95±00.05 (50)	0.85±00.03 (50)	0.79±0.02 (50)	0.67±0.01 (50)	0.66±0.05 (50)
First instar	2.19±0.08 (47)	1.04±0.04 (49)	0.77±0.03 (42)	0.62±0.03 (39)	0.78±0.03 (45)	0.60±0.02 (45)	0.43±0.04 (50)	0.39±0.05 (40)
Second instar	2.04±0.21 (38)	0.94±0.07 (41)	0.60±0.02 (40)	0.66±0.04 (38)	0.73±0.01 (33)	0.61±0.14 (33)	0.70±0.03 (29)	0.40±0.03 (29)
Third instar	1.54±0.04 (30)	0.97±0.04 (29)	0.80±0.05 (39)	0.75±0.04 (34)	0.69±0.04 (30)	0.54±0.03 (30)	0.60±0.06 (24)	0.40±0.03 (27)
Fourth instar	1.88±0.17 (20)	1.16±0.14 (24)	1.32±0.08 (39)	0.96±0.04 (31)	0.61±0.07 (27)	0.84±0.04 (27)	0.46±0.04 (18)	0.62±0.12 (22)
Larva[c]	7.65±0.34 (47)	4.10±0.14 (49)	3.46±0.11 (42)	3.03±0.10 (39)	2.82±0.09 (45)	2.58±0.04 (46)	2.19±0.07 (50)	1.92±0.12 (40)
Prepupa	1.13±0.20 (13)	0.50±0.06 (17)	0.49±0.03 (34)	0.50±0.04 (28)	0.34±0.05 (19)	0.28±0.02 (20)	0.28±0.03 (16)	0.42±0.12 (19)
Pupa	22.21±1.21 (11)	14.96±0.51 (12)	9.87±0.13 (33)	8.80±0.19 (27)	7.07±0.14 (19)	7.36±0.15 (20)	6.42±0.21 (15)	5.63±0.25 (17)
Immature[d]	32.89±1.23 (50)	20.90±0.57 (50)	15.06±0.17 (50)	13.14±0.22 (50)	11.07±0.21 (50)	10.94±0.16 (50)	9.56±0.24 (50)	8.63±0.30 (50)

[a] At 38°C all the parasitoid eggs died before hatching and no evidence of development was observed

[b] In parentheses, number of insects

[c] Combination of instars 1 to 4

[d] Combination of egg, larva, prepupa and pupa

Table 2 Development rates (means±SE) of all stages of *Bracon vulgaris* fed on *Anthonomus grandis* larvae at temperatures from 18°C to 35°C, 70±10% r.h. and photoperiod of 14L/10D determined using Eq. 1 (see text)

Life stage	Temperature (°C)							
	18	20	23	25	28	30	33	35
Egg[a]	0.4812±0.0312 (50)[b]	0.5710±0.0433 (50)	0.9409±0.0998 (50)	1.0000±0.0845(50)	1.3318±0.1788 (50)	1.4310±0.1810 (50)	1.5109±0.1603 (50)	1.7911±0.1203 (50)
First instar	0.5010±0.0411 (47)	1.0020±0.1012 (49)	1.0210±0.1600 (42)	1.2608±0.1567 (39)	2.0010±0.1400 (45)	1.8020±0.1367 (45)	1.8020±0.1797 (50)	1.6908±0.1112 (40)
Second instar	0.6009±0.0712 (38)	1.1701±0.1523 (41)	0.9308±0.0998(40)	1.3710±0.1211 (38)	1.3418±0.1003 (33)	2.1201±0.1203 (33)	1.8910±0.1732(29)	2.0712±0.1503 (29)
Third instar	0.5212±0.0533 (30)	0.5014±0.0711 (29)	0.9401±0.0899(39)	1.3108±0.4412 (34)	1.8404±0.1444 (30)	1.8909±0.1379 (30)	1.8410±0.1598 (24)	2.6900±0.1717 (27)
Fourth instar	0.4401±0.0399 (20)	0.4008±0.0631 (24)	0.6900±0.0777 (39)	1.3914±0.3411 (31)	1.5012±0.1103 (27)	1.5208±0.1201 (27)	1.6709±0.1212 (18)	1.8200±0.1589 (22)
Larva[c]	0.1319±0.0012 (47)	0.1618±0.0087 (49)	0.2201±0.0311 (42)	0.3300±0.0078 (39)	0.4013±0.0700 (45)	0.4412±0.0544 (46)	0.4000±0.0666(50)	0.4901±0.0112 (40)
Prepupa	0.5012±0.0613 (13)	1.0000±0.0488 (17)	1.1910±0.1811 (34)	3.1004±0.1224 (28)	3.9812±0.1711 (19)	3.2715±0.7666 (20)	4.0012±1.0031 (16)	3.5609±0.8891 (19)
Pupa	0.0402±0.0012 (11)	0.0601±0.0099 (12)	0.0809±0.0086 (33)	0.1312±0.0121 (27)	0.1504±0.0039 (19)	0.1603±0.0112 (20)	0.1410±0.0212 (15)	0.1505±0.0077 (17)
Immature[d]	0.0300±0.0010 (50)	0.0412±0.0031 (50)	0.0501±0.0012 (50)	0.0802±0.0099 (50)	0.1010±0.0011 (50)	0.1109±0.0101 (50)	0.1001±0.0013 (50)	0.1001±0.0087 (50)

[a] At 38°C all the parasitoid eggs died before hatching and no evidence of development was observed

[b] In parentheses, number of insects

[c] Combination of instars 1 to 4

[d] Combination of egg, larva, prepupa and pupa

Table 3 Parameters estimated by Sharpe and DeMichele (1977) model (standard errors within parentheses) for development stages of *Bracon vulgaris* fed on *Anthonomus randis* larvae at temperatures from 18°C to 35°C, 70±10% r.h. and photoperiod of 14L/10D

Stage	Parameter					
	RHO^{a}_{25}	H^{b}_{A}	T^{c}_{H}	T^{d}_{H}	R^2	*P value*
Egg	7.0195 (0.4568)	50,389.0000 (438.5430)	291.0000 (31.8310)	45,603.2000 (200.3212)	0.9834	>0.0001
First instar	1.6422 (0.3212)	24,007.7000 (231.3000)	304.4000 (32.8990)	51,075.2000 (99.3200)	0.9164	>0.0003
Second instar	104.3000 (23.3200)	−49,308.3000 (32.3000)	311.0000 (31.5000)	62,709.8000 (132.5000)	0.8432	>0.0009
Third instar	7.4307 (1.9867)	60,629.8000 (110.2100)	292.9000 (32.3000)	52,468.4000 (100.1200)	0.9332	>0.0005
Fourth instar	3.5081 (0.9812)	56,904.4000 (234.0990)	296.0000 (31.786)	56,984.4000 (341.4590)	0.9413	>0.0003
Larva	0.5739 (0.1212)	−3,137.4000 (101.0234)	297.4000 (45.3412)	41,630.2000 (210.5432)	0.9547	>0.0001
Prepupa	6.2715 (1.1678)	71,147.5000 (231.1234)	297.6000 (49.3454)	77,080.8000 (132.7689)	0.9225	>0.0008
Pupa	0.2255 (0.0112)	41,444.8000 199.7688)	298.7000 (76.3421)	52,035.6000 (175.6510)	0.9675	>0.0001
Immature	0.0955 (0.0019)	29,436.8000 (120.5643)	308.9000 (89.1200)	51,332.9000 (123.6599)	0.9749	>0.0001

[a] Development rate at 25°C (298.15° K) assuming no enzyme inactivation

[b] Enthalpy of activation of the reaction that is catalyzed by a rate-controlling enzyme

[c] Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive

[d] Change in the enthalpy associated with high-temperature inactivation of the enzyme

and pupa [$F(1,212)=2.05$; $P=0.101$] stages and that of the first [$F(1,395)=1.95$; $P=-0.109$)], second $F(1,371)=1.22$; $P=0.122$], third [$F(1,264)=1.74$; $P=0.165$] and fourth [$F(1,244)=1.99$; $P=0.199$] instar larvae did not differ significantly between males and females of the parasitoid. Thus, the data for the two sexes were pooled and analyzed together.

The mean development times in days for all stages at all the experimental temperatures are presented in Table 1. At the highest tested temperature (38°C) all the parasitoid eggs died before hatching and no evidence of development was observed. The lethality of this temperature was not instantaneous, and the parasitoids probably died as a consequence of long-term exposure to high temperature stress. High mortality at extreme constant temperatures may result from different mortality agents and inactivation of enzymes (Sharpe and DeMichele 1977).

Table 4 Parameters estimated by Lactin et al. (1995) model (standard errors within parentheses) for development stages of *Bracon vulgaris* fed on *Anthonomus grandis* larvae at temperatures from 18°C to 35°C, 70±10% r.h. and photoperiod of 14L/10D and computation of base temperatures and upper thresholds (°C)

Stage	Parameter				R^2	*P value*	Base temperature	Upper threshold
	ρ^{a}	T^{b}_{L}	Δ^{c}_{T}	λ^{d}				
Egg	0.0517 (0.0012)	52.7056 (0.5612)	10.6923 (0.0112)	−1.4664 (0.1787)	0.9795	>0.0008	8.12	38.53
First instar	0.0551 (0.0019)	41.5447 (0.4532)	5.9402 (1.5432)	−1.9452 (0.3123)	0.9071	>0.0157	9.01	31.68
Second instar	0.0366 (0.0010)	38.5673 (0.8976)	1.4894 (0.8976)	−1.1938 (0.1212)	0.9142	>0.0043	11.80	33.98
Third instar	0.0404 (0.0102)	38.0713 (0.7489)	0.1740 (0.7653)	−1.5536 (0.9812)	0.9461	>0.0002	11.02	37.20
Fourth instar	0.0410 (0.0039)	39.1013 (0.9978)	2.2188 (0.8786)	−1.7114 (0.5453)	0.9371	>0.0020	10.01	33.25
Larva	0.0165 (0.0712)	39.8302 (0.9876)	1.6961 (0.3243)	−1.2155 (0.1213)	0.9530	>0.0010	11.83	33.59
Prepupa	0.0765 (0.0129)	39.4740 (0.7654)	0.0584 (0.0456)	−3.3401 (0.2312)	0.9230	>0.0031	7.09	39.16
Pupa	0.0095 (0.0009)	43.3018 (0.8975)	3.1863 (1.7887)	−1.1470 (0.1289)	0.9600	>0.0007	10.02	31.81
Immature	0.0064 (0.0008)	43.5186 (0.5656)	2.7638 (0.9987)	−1.0956 (0.6759)	0.9710	>0.0003	11.03	32.17

[a] Development rate at 25°C (298.15° K) assuming no enzyme inactivation

[b] Enthalpy of activation of the reaction that is catalyzed by a rate-controlling enzyme

[c] Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive

[d] Change in the enthalpy associated with high-temperature inactivation of the enzyme

The results (Table 1) suggest that *B. vulgaris* is more tolerant than the boll weevil to high temperatures. Therefore, it is expected that *B. vulgaris* will have a higher survivorship than the boll weevil during summer in Brazil. The boll weevils that fed on cotton squares began to experience development stress at 34°C (Bacheler et al. 1975; Sharpe and Hu 1980). In fact, development rates of the boll weevil (Table 2) are similar to those of *Catolaccus grandis* (Burks), a parasitoid of boll weevil, at the same temperatures (Bacheler et al. 1975), showing that the life cycles of this parasitoid and its host are remarkably synchronic. This suggests that both species have physiological adaptations to similar ranges of temperatures (Morales-Ramos and Cate 1993). However, when the boll weevil feeds on cotton bolls, its development times increase significantly (Sharpe and Hu 1980). The boll weevil is, therefore, more available to parasitism when it is developing on cotton bolls than on cotton squares. Fortunately, *B. vulgaris* is better adapted to parasitize boll weevil larvae in cotton bolls.

Bracon mellitor Say, another parasitoid of boll weevil, starts experiencing developmental stress at temperatures close to 38°C (Barfield et al. 1977). Therefore, this parasitoid is as tolerant to high temperature as *B. vulgaris*.

Fit of the models and parameter estimation The high values of R^2 for the models of Sharpe and DeMichele (1977) (Table 3), and Lactin et al. (1995) (Table 4), showed that they are suitable to estimate the development rate of *B. vulgaris* as a function of temperature.

Temperature inhibition was significant only at the high extreme. Low-temperature inhibition was not significant at the lowest temperature tested (18°C);

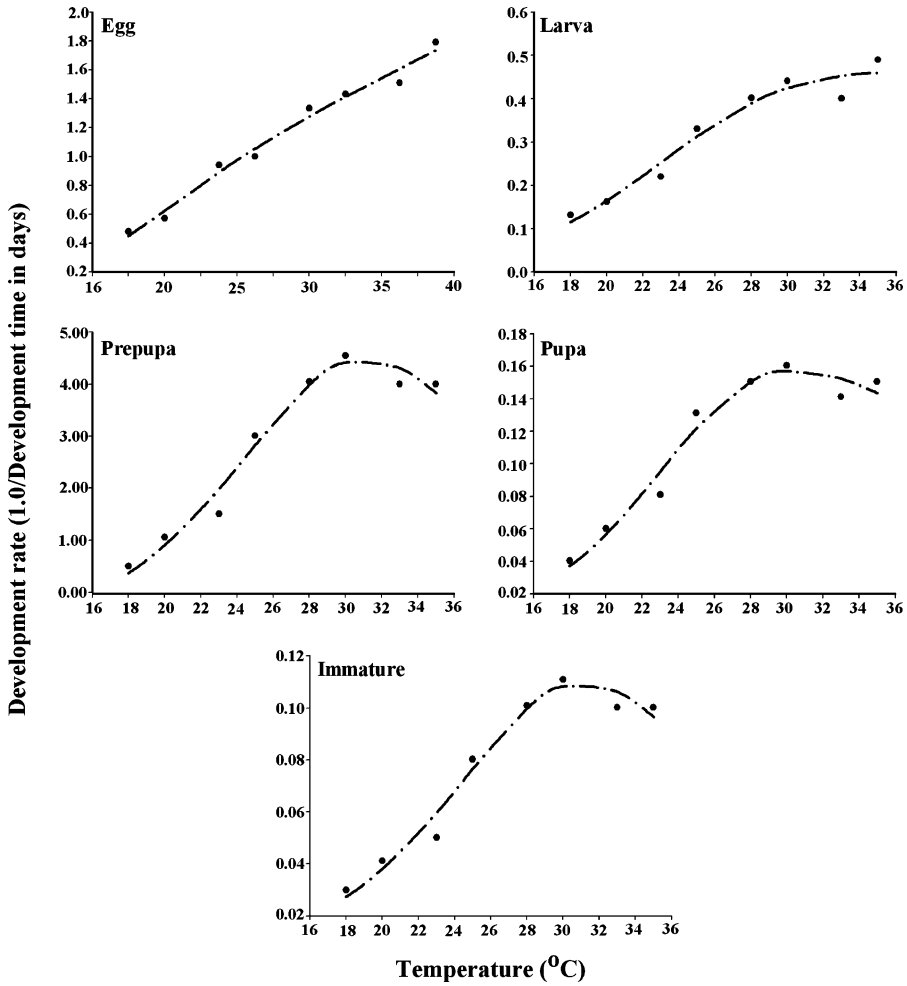

Fig. 1 Relationship between development rate and temperature for development stages of *Bracon vulgaris* fed on *Anthonomus grandis* larvae at temperatures from 18°C to 35°C, 70±10% r.h. and photoperiod of 14L/10D. *Dashed lines*, Sharpe and DeMichele model; *dots*, observed values

therefore, the four-parameter version (without low-temperature inhibition) of the Sharpe and DeMichele (1977) model was used, setting T_L and H_L constant at 100 and 10^8, respectively. The test for low-temperature inhibition is an integral part of the Wagner et al. (1984) SAS program and is based on the degree of deviation from linearity. The linear correlation between development rates and temperature of 30°C and lower was highly significant (r^2=0.9671; $F_{1,4}$=117.63; P= 0.0004), showing no deviation from linearity at the lower temperatures.

The prepupa stage showed the highest tolerance to high temperature, which is represented by the high value of the parameter H_H of the Sharpe and DeMichele (1977) model (Table 3). In the model of Lactin et al. (1995), the high-temperature tolerance of prepupae is shown by the smaller value of Δ_T (Table 4).

The value of T_H for *B. vulgaris* was 308.9°K (Table 3), suggesting this parasitoid will experience thermal stress at 37.75°C. On the other hand, the value of T_H was 307.6°K and 311.7°K for the boll weevil and *B. mellitor*, respectively; therefore, these species are expected to experience thermal stress at 34.45°C and 38.56°C, respectively. *B. vulgaris* appears to have a better tolerance to high temperatures than the boll weevil. It should be pointed out that the characteristics of the Sharpe and DeMichele model tend to predict a thermal maximum that exceeds the maximum observed development rate.

The parameter T_L represents the temperature (°C) at which life can no longer be sustained. The value of this parameter is expressed in degrees Celsius. The value of T_L from the Lactin et al. (1995) model was similar at all development stages of the parasitoid.

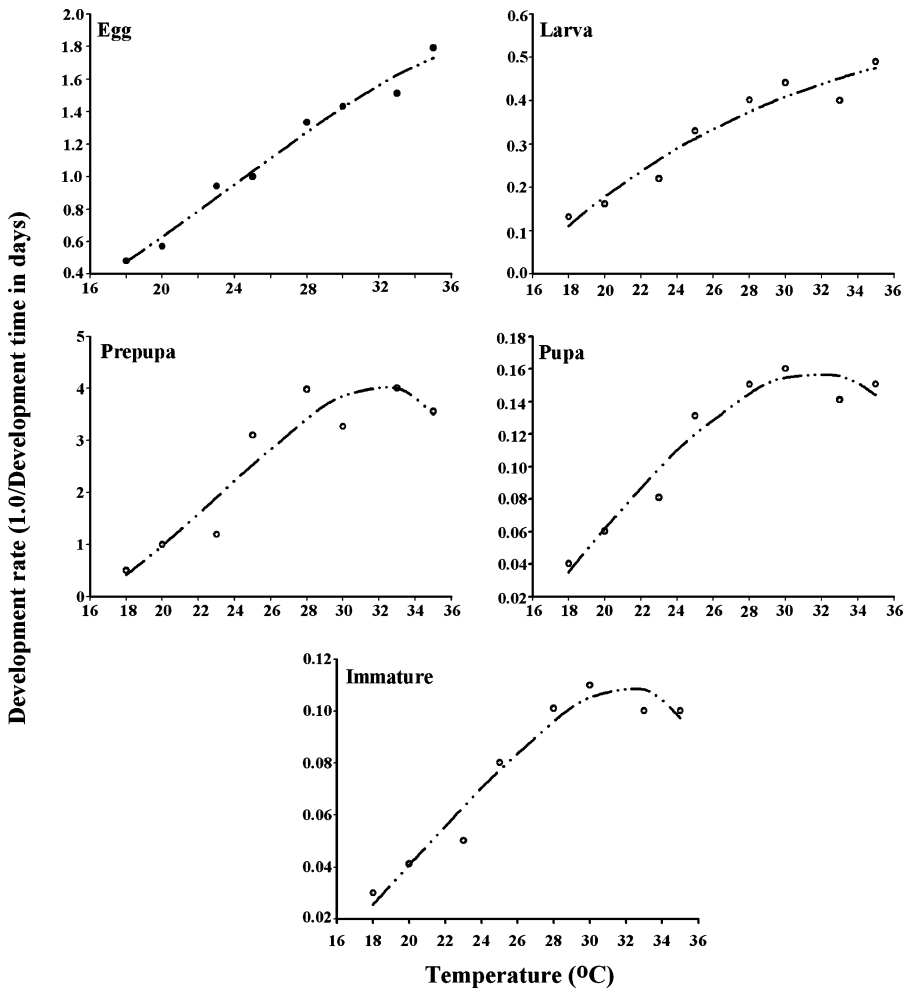

Fig. 2 Relationship between development rate and temperature for development stages of *Bracon vulgaris* fed on *Anthonomus grandis* larvae at temperatures from 18°C to 35°C, 70±10% r.h. and photoperiod of 14L/10D. *Dashed lines*, Lactin et al. model; *dots*, observed values

The estimated value of T_L for the immature stage of *B. vulgaris* was 43.52°C (Table 4). The model of Lactin et al. (1995) showed that *B. vulgaris* is tolerant to high temperatures. The values of λ were below zero, indicating that λ can estimate the threshold for all development stages of *B. vulgaris.* Values estimated by the *x*-intercept method of Wanderley et al. (2007) and by applying the Lactin et al. (1995) model were similar for each development stage of *B. vulgaris* (Table 4). As such, the curvilinear relationship of Lactin et al. (1995) and the regression method may be equivalent descriptive tools for a range of temperatures below the upper thresholds. The values of upper thresholds estimated by the model of Lactin et al. (1995) are presented in Table 3. Therefore, the relationship between development rate and temperature for *B. vulgaris* was appropriately described by the models of Sharpe and DeMichele (1977) (Fig. 1) and Lactin et al. (1995) (Fig. 2).

The estimated values of T_L for the boll weevil, *B. mellitor* and *B. vulgaris* were 39.01°C, 43.51°C, and 43.52°C, respectively. According to the model of Lactin et al. (1995), the two parasitoid species have a greater tolerance to high temperatures than the boll weevil. According to the Sharpe and DeMichele (1977) model (T_H) and the Lactin et al. (1995) model (T_L), *B. vulgaris* experiences thermal stress at 37.5°C and 43.52°C, respectively. According to our results, 38°C is a harmful temperature for *B. vulgaris*, where no development occurred. Therefore, it seems that the Sharpe and DeMichele (1977) model better estimates T_{max} than does the Lactin et al. (1995) model.

The biophysical model of Sharpe and DeMichele (1977) describes a nonlinear response between development rates at low and high temperatures, as well as a linear response at intermediate temperatures. For this reason, Wagner et al. (1984) and Fan et al. (1992) considered that this nonlinear model better describes the effect of constant temperatures on insect development. This model was applied and evaluated by Gould and Elkinton (1990), Orr and Obrycki (1990), Fan et al. (1992), Morales-Ramos and Cate (1993), Harari et al. (1998), and Medeiros et al. (2003) and it was appropriate for determination of the studied development rates.

The two models and the information they provide will be used to determine more accurately the optimal range of conditions for *B. vulgaris* population growth in Brazil. They also will be used to assess other life history characteristics of this parasitoid and similar species now under consideration by the Brazil Department of Agriculture in this multi-state biological control effort.

In summary, both models fit the data (temperature-dependent development rates of *B. vulgaris*) equally well and are equally adequate to simulate development of *B. vulgaris* under conditions of changing temperatures; however, the model of Sharpe and DeMichele (1977) is to be preferred over that of Lactin et al. (1995) to estimate T_{max}. The values of T_H and T_L from the Sharpe and DeMichele model and the Lactin et al. model, respectively, for *B. vulgaris* were higher than that obtained for the boll weevil, indicating a better tolerance of *B. vulgaris* to high temperatures.

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