

## ECOLOGY, BEHAVIOR AND BIONOMICS

### Estimative of *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) Development Time with Non Linear Models

RÔMULO S. MEDEIROS<sup>1</sup>, FRANCISCO S. RAMALHO<sup>2</sup>, JOSÉ E. SERRÃO<sup>3</sup> AND JOSÉ C. ZANUNCIO<sup>1</sup>

<sup>1</sup>Depto. Biologia Animal, Universidade Federal de Viçosa, 36571-000, Viçosa, MG, e-mail: romulo@insecta.ufv.br

<sup>2</sup>Embrapa Algodão, Rua Osvaldo Cruz, 1143, Centenário, C. postal 174, 58107-720, Campina Grande, PB  
e-mail: framalho@cnpa.embrapa.br

<sup>3</sup>Depto. Biologia Geral, Universidade Federal de Viçosa, 36571-000, Viçosa, MG, e-mail: jeserrao@ufv.br

*Neotropical Entomology* 33(2):141-148 (2004)

### Estimativa do Tempo de Desenvolvimento de *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) Através de Modelos Não Lineares

RESUMO - O objetivo deste estudo foi avaliar a precisão dos modelos não lineares de Davidson (1942, 1944), Stinner *et al.* (1974), Sharpe & DeMichele (1977) e Lactin *et al.* (1995) no estudo da relação entre as taxas de desenvolvimento das diferentes fases de *Podisus nigrispinus* (Dallas) e a temperatura. Os menores valores de R<sup>2</sup> para os modelos de Davidson (0,1593 a 0,2672, e de 0,1406 a 0,2804 para machos e fêmeas, respectivamente) e de Stinner *et al.* (0,2136 a 0,6389, e de 0,1417 a 0,3045 para machos e fêmeas, respectivamente), indicaram que esses modelos não são adequados para a estimativa do tempo de desenvolvimento de *P. nigrispinus*, em função da temperatura. Entretanto, os altos valores de R<sup>2</sup> para os modelos de Sharpe & DeMichele (0,9226 a 0,9893, e de 0,8818 a 0,9914 para machos e fêmeas, respectivamente), e de Lactin *et al.* (0,9485 a 0,9997, e de 0,8961 a 0,9997 para machos e fêmeas, respectivamente), indicaram que esses modelos são adequados para a estimativa do tempo de desenvolvimento de *P. nigrispinus*, em função da temperatura. Fêmeas de *P. nigrispinus*, na fase imatura, mostraram maior tolerância à alta temperatura, a qual é representada pelo parâmetro  $H_H$  obtido do modelo de Sharpe & DeMichele. De acordo com este modelo, fêmeas de *P. nigrispinus* na fase imatura apresentam estresse térmico a 33,3°C, indicando que a estimativa da ação térmica máxima foi bastante realista.

PALAVRAS-CHAVE: Asopinae, controle biológico, *Alabama argillacea*, taxa de desenvolvimento, predador

ABSTRACT - The objective of this study was to evaluate the precision of the non linear models of Davidson (1942, 1944), Stinner *et al.* (1974), Sharpe & DeMichele (1977), and Lactin *et al.* (1995) to describe relationship between developmental rate of different stages of *Podisus nigrispinus* (Dallas) and temperature. Lower values of R<sup>2</sup> for the models of Davidson (0.1593 to 0.2672, and 0.1406 to 0.2804 for males and females, respectively) and of Stinner *et al.* (0.2136 to 0.6389, and 0.1417 to 0.3045 for males and females, respectively) showed that these models were not adequate to estimate developmental rate of *P. nigrispinus* as function of temperature. However, high values of R<sup>2</sup> for the models of Sharpe & DeMichele (0.9226 to 0.9893, and 0.8818 to 0.9914 for males and females, respectively), and of Lactin *et al.* (0.9485 to 0.9997, and 0.8961 to 0.9997 for males and females, respectively) showed that these models are suitable to estimate developmental rate of *P. nigrispinus* as function of temperature. Females of *P. nigrispinus* showed high tolerance to high temperature which is represented by high values of  $H_H$  for immature stage of this insect obtained with the Sharpe & DeMichele model. According to this model females of *P. nigrispinus* present thermal stress at 33.3°C, which indicates that maximum thermal estimated by this model was close to the real one.

KEY WORDS: Asopinae, biological control, *Alabama argillacea*, developmental rate, predator

*Podisus nigrispinus* (Dallas) is a generalist predator which occurs in many countries of Central and South America (Thomas 1992) as an important biological control agent in several crops. Michel (1994) emphasized the

importance of this predator against *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) in Paraguay. The occurrence of this predator in Brazil is mentioned in many crops of economic importance such as tomato

(*Lycopersicum esculentum* Mill.) (Bergam *et al.* 1984), soybean (*Glycine max* L.) (Panizzi *et al.* 1977), and cotton (*Gossypium hirsutum* L.) (Medeiros *et al.* 1998). For this reason, studies with this predator have been showing its potential to control populations of *A. argillacea* (Santos *et al.* 1995, 1996, Medeiros *et al.* 2000, 2003, Lemos *et al.* 2001).

The relationship between developmental rate of insects and temperature represents an important ecological tool to modelling population dynamics of these organisms (Uvarov 1931, Howe 1967). Several authors (Davidson 1942, 1944, Stinner *et al.* 1974, Sharpe & DeMichele 1977, Lactin *et al.* 1995) have formulated mathematical models to describe the relationship between developmental rate of insects and temperature. The knowledge of such relationships is important to determine seasonal occurrences of insect populations as strategies for integrated pest management (Marco *et al.* 1997).

Linear models were the first ones developed for insects (Howe 1967). However, the lack of linearity of the developmental rate of insects at low and high temperatures suggests that these models are inadequate to describe such parameters for these organisms. This has led to increasing development of non linear phenological models in programs of integrated pest management from the beginning of 1980 (Wagner *et al.* 1984, Worner 1992).

Non linear models (Logan *et al.* 1976, Hilbert & Logan 1983) have been developed for different species of insects submitted to certain circumstances. Davidson (1942, 1944) described developmental rate of insects as function of temperature through the use of logistic equations. Stinner *et al.* (1974) described the effect of temperature on developmental rate as a modified sigmoid equation which results in a symmetrical curve at high temperatures. Sharpe & DeMichele (1977) formulated a complex biophysical model, later modified by Schoolfield *et al.* (1981), which describes a non linear response of developmental rate of insects exposed to low and high temperatures as well as a linear response at intermediate temperatures. Lactin *et al.* (1995) modified the non linear model of Logan *et al.* (1976) by eliminating the parameter  $\psi$ , which is the direct measurable rate of the temperature-dependent physiological process at  $T_b$ , and introducing the parameter intercept  $\lambda$  which allowed the estimative of developmental threshold.

Linear models can not supply precise information on inhibition of development at extreme temperatures and, with a few exceptions, they have been applied to study such rates for insect pest species as function of temperature but not of their natural enemies (Gould & Elkinton 1990). For this reason, the purpose of this research was to determine which non linear model (Davidson, 1942, 1944, Stinner *et al.* 1974, Sharpe & DeMichele 1977, Lactin *et al.* 1995) can better describe the effect of temperature on *P. nigrispinus* development.

## Material and Methods

The research was developed at the Biological Control Unit (BCU)/Embrapa Algodão, in Campina Grande, State of Paraíba, Brazil. Data used were obtained from Medeiros *et al.* (1998). The developmental rate from egg to adult was studied under

the following constant temperatures: 17, 20, 23, 25, 28, 30, 33, and 35°C (60 ±10% RH, and a photoperiod of 14:10 [L:D] h).

Mean developmental rate of *P. nigrispinus* at different temperatures was estimated with the formula:

$$r(T) = 1.0 / e^{\left\{ \left[ \frac{\sum_{i=1}^n \ln(di)}{n} \right] \right\}} \quad (1)$$

where  $r(T)$  is the mean developmental rate at temperature  $T$  (°C),  $di$ , individual observations of developmental time in days, and  $n$ , number of observations. This method is recommended by Logan *et al.* (1976) to account for linearity in the transformation from developmental time to developmental rate.

Developmental rate is the reciprocal of developmental time in days and it is represented by values from 0 to 1. These rates are used in developmental models where data are added each day. The development of an organism is completed when the sum of their daily rate of development reaches value 1 (Curry & Feldman 1987). Therefore, the integral of the function of developmental rate along time (as the models of Davidson, 1942, 1944, Stinner *et al.* 1974, Sharpe & DeMichele 1977, Lactin *et al.* 1995) can be used to simulate the development of an organism submitted to changes in temperature. For this reason, descriptive non linear procedures have been used to analyse relationship between developmental rate of *P. nigrispinus* and temperature as described:

Logistic equation of Davidson (1942, 1944):

$$r(T) = \frac{k}{1 + e^{-a-bT_i}} \quad (2)$$

where  $r(T)$  is the mean developmental rate at temperature  $T$  (°C),  $a$ , value which defines the place of the regression line in relation to the  $x$  axis,  $b$ , the slope of curve line,  $k$ , a constant defining the upper limit of the sigmoid line,  $T_i$ , temperature in environmental chamber. Parameters  $a$ ,  $b$  and  $k$  were estimated with regression of non linear model of Marquardt with the PROC NLIN (Sas Institute Inc. 2000). This method is used to determine the minimum square of the parameters estimated with this model.

Sigmoid equation of Stinner *et al.* (1974):

$$r(T) = \frac{c}{1 + e^{k_1 + k_2 T}} \quad (3)$$

where  $r(T)$  is the mean developmental rate at temperature  $T$  (°C),  $c$ ,  $(1/T_{max}) \times (e^{k_1 + k_2 T_{max}})$  (asymptote),  $k_1$  and  $k_2$ , empirical constants and  $T' = T$ , for  $T < T_{max}$  and  $T' = 2 \times T_{max} - T$ , for  $T > T_{max}$ . The parameters  $c$ ,  $k_1$  and  $k_2$  were estimated by Marquardt's method using PROC NLIN (Sas Institute Inc. 2000).

Sharpe & DeMichele (1977) biophysical model, modified by Schoolfield *et al.* (1981):

$$r(T) = \frac{RHO_{25} \left( \frac{T}{298.15} \right) \exp \left[ \left( \frac{H_A}{R} \right) \left( \frac{1}{298.15} - \frac{1}{T} \right) \right]}{1 + \exp \left[ \left( \frac{H_L}{R} \right) \left( \frac{1}{T_L} - \frac{1}{T} \right) \right] + \exp \left[ \left( \frac{H_H}{R} \right) \left( \frac{1}{T_H} - \frac{1}{T} \right) \right]} \quad (4)$$

where  $r(T)$  is the mean developmental rate at temperature  $T$  (°K),  $R$ , universal gas constant (1.987 cal degree<sup>-1</sup>mole<sup>-1</sup>),

$RHO_{25}$ , the developmental 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 Inc. 2000) with the procedure adopted by Wagner *et al.* (1984).

The numerator of the fourth equation explains the dependent developmental 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). These authors developed a method to determine if data are adjusted by a model constituted of six, four or two parameters. This method tests the non linearity 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 both extreme temperatures have significant effect in the inhibition. When high temperatures have no significant effect in the inhibition, the parameters  $T_H$  and  $H_H$  will assume constant values of 1,000 and 100,000,000, respectively. If low temperature has no significant effect in the inhibition, the parameters  $T_L$  and  $H_L$  will receive constant values of 100 and -100,000,000, respectively. Therefore, in both cases, the model constituted of four parameters will be better adjusted to the data. When low and high temperatures have no effect in the inhibition, the model with two parameters will be better adjusted to the data; then, the four parameters  $T_H$ ,  $H_H$ ,  $T_L$  and

$H_L$  will receive constant values of 1,000; 100,000,000; 100, and -100,000,000, respectively.

Model of Lactin *et al.* (1995) resulted from the modification of the non linear model of Logan *et al.* (1976):

$$r(T) = e^{\rho T} - e^{\left[ \rho T_L - \left( \frac{T_L - T}{\Delta T} \right) \right]} + \lambda \quad (5)$$

where  $r(T)$  is the mean developmental rate at temperature  $T$  (°C),  $T_L$ , lethal temperature (°C),  $r$ , rate of increase at optimal temperature,  $DT$ , difference between lethal and optimal temperature of development, and  $\lambda$ , the parameter that makes the curve intercept the  $x$ -axis, allowing to estimate developmental threshold. Parameters  $T_L$ ,  $r$ ,  $DT$  and  $\lambda$  were estimated by Marquardt's method using PROC NLIN (Sas Institute Inc. 2000).

$R^2$  of these models were calculated as  $R^2 = 1 - (S_y^2 / S_{ud}^2)$ , where  $S_y^2$  is the variance of the residues of the model and  $S_{ud}^2$  is the variance of means of developmental rates.

### Results

Except for some instars [2<sup>nd</sup> (30°C), 3<sup>rd</sup> (30°C and 33°C), 4<sup>th</sup> (33°C) and 5<sup>th</sup> (28°C and 33°C) of *P. nigrispinus* that originated males; and 1<sup>st</sup> (30°C), 4<sup>th</sup> (33°C) and 5<sup>th</sup> (28°C) instars for those that originated females], developmental rates of this insect increased as the temperature rose (Table 1). On the other hand, developmental rates of eggs and nymphs of *P. nigrispinus* increased as the temperature rose for both sexes (Table 2). At the highest tested temperature (35°C) all the predator eggs died before hatching and no evidence of development was observed. Therefore, the development time at 35°C was not feasible because of the deleterious effect this constant high temperature had on the eggs of this predator. The lethality of this temperature was not instantaneous, and the predators probably died as a consequence of long time

Table 1. Mean developmental rates of each instar of *P. nigrispinus* fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10.

Temperature <sup>1</sup> (°C)	Instar					
	First	Second	Third	Fourth	Fifth	
	Male					
17	0.1039	0.0909	0.0860	0.0897	0.0652	
20	0.1779	0.1665	0.1897	0.1715	0.1039	
23	0.2806	0.2179	0.2814	0.2449	0.1471	
25	0.3288	0.2723	0.3199	0.2542	0.1692	
28	0.4414	0.3260	0.4278	0.3239	0.1596	
30	0.4811	0.3140	0.4125	0.3456	0.1699	
33	0.5000	0.5000	0.3333	0.3333	0.1667	
	Female					
17	0.0991	0.1006	0.1151	0.0736	0.0576	
20	0.1732	0.1573	0.1813	0.1664	0.0980	
23	0.2987	0.2224	0.2665	0.2346	0.1359	
25	0.3292	0.2718	0.2854	0.2601	0.1409	
28	0.4791	0.3236	0.3894	0.3017	0.1251	
30	0.4673	0.3250	0.4299	0.3304	0.1320	
33	0.5000	0.5000	0.5000	0.2500	0.2000	

<sup>1</sup>At 35°C all the predator eggs died before hatching and no evidence of development was observed.

Table 2. Mean developmental rates of *P. nigrispinus* males and females fed with *A. argillacea* larvae at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10.

Temperature <sup>1</sup> (°C)	Stage		
	Egg	Nymph	Immature
Male			
17	0.0702	0.0170	0.0137
20	0.1154	0.0309	0.0244
23	0.1743	0.0439	0.0350
25	0.1972	0.0505	0.0402
28	0.2502	0.0582	0.0472
30	0.2816	0.0595	0.0490
33	0.3295	0.0625	0.0525
Female			
17	0.0702	0.0167	0.0135
20	0.1154	0.0294	0.0234
23	0.1743	0.0427	0.0343
25	0.1972	0.0466	0.0377
28	0.2502	0.0517	0.0428
30	0.2816	0.0540	0.0452
33	0.3395	0.0667	0.0554

<sup>1</sup>At 35°C all the predator eggs died before hatching and no evidence of development was observed.

exposure to high temperature stress. High mortality at extreme constant temperatures may result from different mortality agents and inactivation of enzymes (Sharpe & DeMichele 1977).

Low values of R<sup>2</sup> of the logistic model of Davidson (1942, 1944) (from 0.1593 to 0.2672, and 0.1406 to 0.2804 for males and females, respectively) (Table 3) and for the sigmoid model of Stinner *et al.* (1974) (from 0.2136 to 0.6389, and from 0.1417 to 0.3045 for males and females, respectively) (Table 4) indicate that these models are not adjusted for the data obtained for *P. nigrispinus*.

Inhibition of *P. nigrispinus* development occurred at the highest temperature (35°C) while in the lowest temperature (17°C) this was not significant. Since the inhibition of developmental rate of this predator was only significant at higher temperature, we used the version of Sharpe & DeMichele (1977) model, with constants  $T_L$  and  $H_L$  assuming the values of 100 and -100,000,000, respectively. Linear correlation between developmental rate and temperature up to 33°C was significant (as for instance, immature males: R<sup>2</sup> = 0.95; F = 99.76; df = 1,5; P = 0.0002 and immature females: R<sup>2</sup> = 0.97; F = 187.19; df = 1,5; P = 0.0001) with no deviation in linearity at lower temperatures.

High values of R<sup>2</sup> for the biophysical model of Sharpe & DeMichele (1977) (from 0.9226 to 0.9893, and from 0.8818 to 0.9914 for males and females, respectively) (Table 5) and for the model of Lactin *et al.* (1995) (from 0.9485 to 0.9997, and from 0.8961 to 0.9997 for males and females, respectively) (Table 6) indicate good adjustment of these models for data of developmental rate of *P. nigrispinus*.

Females of *P. nigrispinus* showed great tolerance to high temperature, which is represented by high value of  $H_H$  for the immature stage (Table 5) obtained with the model of Sharpe & DeMichele (1977).

Table 3. Parameters estimated by Davidson's (1942, 1944) model for developmental stages of *P. nigrispinus* fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10.

Stage	Parameter			R <sup>2</sup>
	k <sup>1</sup>	a <sup>2</sup>	b <sup>3</sup>	
Male				
Egg	0.2136	8.7455	0.4558	0.2382
1 <sup>st</sup> instar	0.3527	9.5165	0.4868	0.2672
2 <sup>nd</sup> instar	0.2842	8.3711	0.4386	0.2129
3 <sup>rd</sup> instar	0.2983	11.6787	0.6333	0.2567
4 <sup>th</sup> instar	0.2521	10.5903	0.5801	0.2240
5 <sup>th</sup> instar	0.1346	11.2127	0.6507	0.1593
Nymph	0.0461	10.4527	0.5733	0.2219
Immature	0.0378	10.0637	0.5477	0.2263
Female				
Egg	0.2136	8.7455	0.4558	0.2382
1 <sup>st</sup> instar	0.3583	10.2465	0.5210	0.2804
2 <sup>nd</sup> instar	0.2869	8.0000	0.4190	0.2076
3 <sup>rd</sup> instar	0.3250	8.2045	0.4322	0.2219
4 <sup>th</sup> instar	0.2103	12.6699	0.7072	0.1790
5 <sup>th</sup> instar	0.1220	11.8308	0.6855	0.1406
Nymph	0.0440	10.1160	0.5571	0.2072
Immature	0.0363	9.7670	0.5332	0.2155

<sup>1</sup>Constant defining the upper limit of the sigmoid line

<sup>2</sup>Value defining the place of the regression line in relation to the x axis

<sup>3</sup>Slope of the curve line

Table 4. Parameters estimated by Stinner *et al.*'s (1974) model for developmental stages of *P. nigrispinus* fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10.

Stage	Parameter			R <sup>2</sup>
	c <sup>1</sup>	k <sub>1</sub> <sup>2</sup>	k <sub>2</sub> <sup>3</sup>	
Male				
Egg	0.2136	8.7453	0.4558	0.2382
1 <sup>st</sup> instar	0.3524	9.5228	0.4872	0.2669
2 <sup>nd</sup> instar	0.2839	8.3819	0.4393	0.2136
3 <sup>rd</sup> instar	0.2987	11.8677	0.6327	0.2391
4 <sup>th</sup> instar	0.2526	10.5661	0.5785	0.2231
5 <sup>th</sup> instar	0.1403	- 1626.6000	46.8227	0.6389
Nymph	0.0461	10.4605	0.5738	0.2219
Immature	0.0378	10.0613	0.5775	0.2263
Female				
Egg	0.2136	8.7453	0.4558	0.2382
1 <sup>st</sup> instar	0.3581	10.2533	0.5214	0.3045
2 <sup>nd</sup> instar	0.2866	8.0084	0.4196	0.2079
3 <sup>rd</sup> instar	0.3247	8.2116	0.4327	0.2215
4 <sup>th</sup> instar	0.2101	12.7014	0.7091	0.1783
5 <sup>th</sup> instar	0.1217	11.8817	0.6887	0.1417
Nymph	0.0440	10.1163	0.5571	0.2072
Immature	0.0364	9.7575	0.5327	0.2155

<sup>1</sup>( $1/t_{max}$ ) x ( $e^{k_1} + k_2 T_{max}$ ) (asymptote)

<sup>2</sup>Empirical constant

<sup>3</sup>Empirical constant

The parameter  $T_H$  of the model of Sharpe & DeMichele (1977) represents the temperature (°K) in which the enzyme that controls developmental rate of the insect is partially inactivated. The values of the parameter  $T_H$  were similar in all developmental stages of the *P. nigrispinus*. The values of  $T_H$  for *P. nigrispinus* males and females were of 306.3°K and 306.4°K (Table 5). Therefore, this species will experience thermal stress at 33.3°C. This indicates that the estimate of the maximum thermal action for the model of Sharpe & DeMichele (1977) was quite realistic.

The parameter  $T_L$  of the model of Lactin *et al.* (1995) represents the temperature (°C) at which life can no longer be sustained. The value of this parameter is expressed in degree Celsius. The values of  $T_L$  were similar in all developmental stages of the predator. The estimated values of  $T_L$  for males and females of *P. nigrispinus* were 37.80 and 35.38°C, respectively (Table 6). The model of Lactin *et al.* (1995) showed that males of *P. nigrispinus* are more tolerant to high temperatures than females of this species. Values of  $l$  were lower than zero, indicating that it can estimate the threshold for all developmental stages of *P. nigrispinus*. Therefore, relationship between developmental rate and temperature for males and females of *P. nigrispinus* was appropriately described by the models of Sharpe & DeMichele (1977) and of Lactin *et al.* (1995) (Figs. 1 and 2).

**Discussion**

Medeiros *et al.* (1998) reported that *P. nigrispinus* maintained its population in the cotton crop in the State of

Paraíba, Brazil, during all cotton season in conditions of prey scarcity (after outbreaks of *A. argillacea*) and at temperatures that can reach 35°C. However, these authors reported that *P. nigrispinus* presented low survival at 33°C in laboratory conditions and no development at 35°C. It is probable that high mortality at extreme constant temperatures may be the result from different mortality agents and inactivation of enzymes (Sharpe & DeMichele 1977). Similar results were obtained by Didonet *et al.* (1995). It is possible that the development of *P. nigrispinus* in areas where maximum temperatures exceed the lethal one can be explained by oscillations of temperature during the day and to the microclimate produced by the agroecosystem of cotton plants. High mortality in experiments with insect maintained at extreme and constant temperatures may not reflect its real response to natural conditions of temperature fluctuation (Logan *et al.* 1985, Torres *et al.* 1998) because the insect can receive strong radiation during the day and mild temperatures at night (Worner 1992). Besides, the lethal effect of extreme temperatures depends on length of the period of maintainance of the insect in those temperatures (Howe 1967).

The non linear logistic model of Davidson (1942, 1944) and the sigmoid model of Stinner *et al.* (1974) have not appropriately described the relationship between developmental rates of different stages of *P. nigrispinus* and the temperature. Wagner *et al.* (1984) stated that the models to describe the relationship between developmental rate and temperature of different species of insects have the followings problems: (1) the model of Stinner *et al.* (1974) assumes symmetrical form on both sides of the optimal temperature and for this reason does not describe,

Table 5. Parameters estimated by Sharpe & DeMichele's (1977) model for developmental stages of *P. nigrispinus* fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10.

Stage	Parameter				R <sup>2</sup>
	RHO <sub>25</sub> <sup>1</sup>	H <sub>A</sub> <sup>2</sup>	T <sub>H</sub> <sup>3</sup>	H <sub>H</sub> <sup>4</sup>	
Male					
Egg	0.1883	15197.40	306.30	1866674.00	0.9893
1 <sup>st</sup> instar	0.3126	16819.20	306.30	1310962.00	0.9855
2 <sup>nd</sup> instar	0.2435	14727.50	307.50	4419068.00	0.9640
3 <sup>rd</sup> instar	0.2983	14847.90	306.20	680026.00	0.9461
4 <sup>th</sup> instar	0.2484	13256.30	306.30	1208193.00	0.9697
5 <sup>th</sup> instar	0.1415	8879.00	306.30	1249946.00	0.9226
Nymph	0.0452	12248.60	306.30	1313382.00	0.9393
Immature	0.0364	12756.60	306.30	1394342.00	0.9671
Female					
Egg	0.1883	15197.40	306.30	1866674.00	0.9893
1 <sup>st</sup> instar	0.3192	16597.30	306.30	1169250.00	0.9639
2 <sup>nd</sup> instar	0.2452	14699.40	307.50	4282544.00	0.9741
3 <sup>rd</sup> instar	0.2882	15034.90	306.30	1880428.00	0.9914
4 <sup>th</sup> instar	0.2152	15057.90	306.20	1262034.00	0.8818
5 <sup>th</sup> instar	0.1222	8833.10	307.50	4203392.00	0.8902
Nymph	0.4200	11180.70	306.40	2095507.00	0.9598
Immature	0.0343	11848.40	306.40	2032902.00	0.9672

<sup>1</sup>Developmental rate at 25°C (298.15°K), assuming no enzyme inactivation.

<sup>2</sup>Enthalpy of activation of the reaction that is catalyzed by a rate-controlling enzyme.

<sup>3</sup>Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive.

<sup>4</sup>Change in the enthalpy associated with high-temperature inactivation of the enzyme.

Table 6. Parameters estimated by Lactin *et al.*'s (1995) model for developmental stages of *P. nigrispinus* fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10.

Stage	Parameter				R <sup>2</sup>
	$\rho^1$	T <sub>L</sub> <sup>2</sup>	$\Delta t^3$	$\lambda^4$	
			Male		
Egg	0.0122	35.7545	0.5327	- 1.1589	0.9997
1 <sup>st</sup> instar	0.0193	36.1643	1.0723	- 1.2852	0.9983
2 <sup>nd</sup> instar	0.0153	35.1515	0.1239	- 1.2059	0.9600
3 <sup>rd</sup> instar	0.0204	37.6417	2.4067	- 1.3193	0.9930
4 <sup>th</sup> instar	0.0143	36.6508	1.3153	- 1.1693	0.9896
5 <sup>th</sup> instar	0.0073	37.4386	1.4257	- 1.0518	0.9485
Nymph	0.0032	37.9238	1.1182	- 1.0356	0.9969
Immature	0.0027	37.7986	0.9981	- 1.0303	0.9978
			Female		
Egg	0.0122	35.7545	0.5327	- 1.1589	0.9997
1 <sup>st</sup> instar	0.0199	36.2738	1.1864	- 1.3010	0.9857
2 <sup>nd</sup> instar	0.0154	35.1431	0.1175	- 1.2048	0.9682
3 <sup>rd</sup> instar	0.0204	37.6417	2.4067	- 1.3193	0.9930
4 <sup>th</sup> instar	0.0143	36.6508	1.3153	- 1.1693	0.9896
5 <sup>th</sup> instar	0.0058	35.2014	0.1094	- 1.0309	0.8961
Nymph	0.0027	35.3631	0.1336	- 1.0259	0.9799
Immature	0.0023	35.3829	0.1326	- 1.0239	0.9862

<sup>1</sup>Rate of increase at optimal temperature

<sup>2</sup>Lethal temperature (°C)

<sup>3</sup>Difference between the lethal and optimal temperature of development

<sup>4</sup>Parameter that makes the curve intercept the *x*-axis, allowing the estimation of a developmental threshold.

appropriately, the development of insects at high temperatures; and (2) the model of Davidson (1942, 1944) has low descriptive precision at both final of the curves of the relationship between developmental rate and temperature. Harari *et al.* (1998) have pointed out that the model of Davidson (1942, 1944) do not appropriately estimate the optimal temperature for development of *Maladera matrida* Argaman (Coleoptera: Scarabaeidae) because it estimated longer developmental rates at higher than at optimal temperatures.

The biophysical model of Sharpe & DeMichele (1977) describes a non linear response between developmental 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) consider that this non linear model better describes the effect of constant temperatures on insects development. This model was applied and evaluated by Gould & Elkinton (1990), Orr & Obrycki (1990), Fan *et al.* (1992), Morales-Ramos & Cate (1993), Judd & McBrien (1994) and Harari *et al.* (1998) and it was appropriate for determination of developmental rates studied.

Lactin *et al.* (1995), modified the non linear model of Logan *et al.* (1976), by eliminating the parameter Y and introducing the parameter I (intercept), which allowed to estimate developmental threshold of insects. This model was applied and evaluated by Briere & Pracros (1998) and it is appropriate to describe relationship between developmental rate of different stages of *Lobesia botrana* Dennis & Schifferrmüller (Lepidoptera: Tortricidae) and temperature.

The models of Sharpe & DeMichele (1977) and of Lactin *et al.* (1995) described, appropriately, the relationship between

developmental rates of different stages of males and females of *P. nigrispinus* and the temperature (Figs. 1 and 2) because both described an asymmetrical form around high temperature. Briere & Pracros (1998) stated that the relationship between developmental rate and temperature in insects is not linear, and it presents asymmetrical form being composed by three sections: the first is represented by low temperatures, where the increase on developmental rate is not linear from the point of development zero; second section is where the developmental rate becomes proportional to temperature increase; and the third begin from optimal until lethal temperature. Our results suggest that the models of Sharpe & DeMichele (1977) and of Lactin *et al.* (1995) are appropriate to describe relationship between developmental rates of different instars and stages of *P. nigrispinus* and temperature.

### Acknowledgments

To the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), to the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and to the staff of the Biological Control Unit/Embrapa Algodão.

### Literature Cited

Bergam, E.C., S.O. Imenes, D. Hojo, T.B. Campos, A.P. Takemitsu & M.L.F.S. Macellaro. 1984. Levantamento da entomofauna na cultura do tomateiro (*Lycopersicon esculentum*). *Biológico* 50: 209-236.

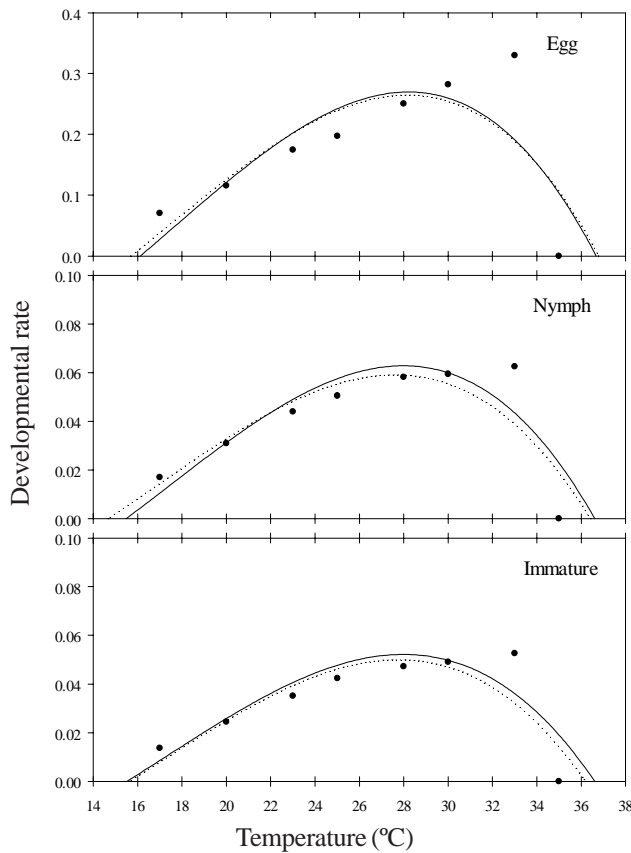


Figure 1. Relationship between developmental rate and temperature for developmental stages of *P. nigrispinus* males fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10. Lactin *et al.* model (—); Sharpe & DeMichele model (.....); observed value (●).

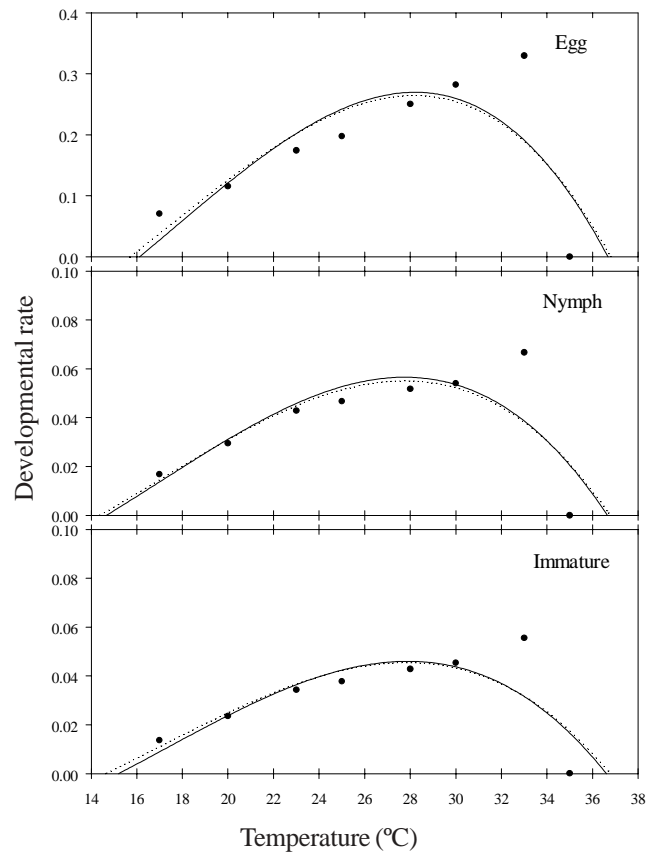


Figure 2. Relationship between developmental rate and temperature for developmental stages of *P. nigrispinus* females fed with *A. argillacea* larvae, at temperatures from 17°C to 35°C, relative humidity of 60 ± 10%, and photoperiod of L:D 14:10. Lactin *et al.* model (—); Sharpe & DeMichele model (.....); observed value (●).

**Briere, J.F. & P. Pracros. 1998.** Comparison of temperature-dependent growth models with the development of *Lobesia botrana* (Lepidoptera: Tortricidae). *Environ. Entomol.* 27: 94-101.

**Curry, G.L. & R.M. Feldman. 1987.** Mathematical foundations of population dynamics. TEES Monograph Series, College Station, Texas. 249p.

**Davidson, J. 1942.** On the speed of development of insect eggs at constant temperatures. *Aust. J. Exp. Biol. Med. Sci.* 20: 233-239.

**Davidson, J. 1944.** On the relationship between temperature and rate of development of insects at constant temperatures. *J. Anim. Ecol.* 13: 26-38.

**Didonet, J.C., J.C. Zanuncio, C.S. Sedyama M.C. Picanço. 1995.** Desenvolvimento e sobrevivência ninfal de *Podisus nigrispinus* (Dallas) e *Supputius cincticeps* (Stal) (Heteroptera: Pentatomidae) em diferentes temperaturas. *Rev. Bras. Zool.* 12: 513-518.

**Fan, Y., E. Groden & F.A. Drummond. 1992.** Temperature-dependent development of the Mexican bean beetle (Coleoptera: Coccinellidae) under constant and variable temperatures. *J. Econ. Entomol.* 85: 1762-1770.

**Gould, J.R. & J.S. Elkinton. 1990.** Temperature-dependent growth of *Cotesia melanoscela* (Hymenoptera: Braconidae), a parasitoid of the gypsy moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* 19: 859-865.

**Harari, A.R., D. Ben-Yakir, M. Chen & D. Rosen. 1998.** Temperature-dependent developmental models for predicting the phenology of *Maladera matrida* (Coleoptera: Scarabaeidae). *Environ. Entomol.* 27: 1220-1228.

**Hilbert, D.W. & J.A. Logan. 1983.** Empirical model of nymphal development for the migratory grasshopper, *Melanoplus sanguinipes* (Orthoptera: Acrididae). *Environ. Entomol.* 12: 1-5.

**Howe, R.W. 1967.** Temperature effects on embryonic development in insects. *Ann. Rev. Entomol.* 10: 15-42.

- Lactin, D.J., N.J. Holliday, D.L. Johnson & R. Craigen. 1995.** Improved rate model of temperature-dependent development by arthropods. *Environ. Entomol.* 24: 68-75.
- Logan, J.A., D.J. Wollkind, S.C. Hoyt & L.K. Tanigoshi. 1976.** An analytic model for description of temperature dependent rate phenomena in arthropods. *Environ. Entomol.* 5: 1133-1140.
- Logan, J.A., R.A. Casagrande, H.H. Faubert & F.A. Drummond. 1985.** Temperature-dependent development and feeding of immature Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *Environ. Entomol.* 14: 275-283.
- Judd, G.J.R. & H.L. McBrien. 1994.** Modeling temperature-dependent development and hatch of overwintered eggs of *Campylomma verbasci* (Heteroptera: Miridae). *Environ. Entomol.* 23: 1224-1234.
- Lemos, W.P., R.S. Medeiros, F.S. Ramalho & J.C. Zanuncio. 2001.** Effects of plant feeding on the development, survival, and reproduction of *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae). *Int. J. Pest Manag.* 47: 89-93.
- Marco, V., A. Taberner & P. Castañera. 1997.** Development and survival of immature *Aubeonymus mariaefrancisciae* (Coleoptera: Curculionidae) at constant temperatures. *Ann. Entomol. Soc. Amer.* 90: 169-176.
- Medeiros, R.S., F.S. Ramalho, W.P. Lemos & J.C. Zanuncio. 2000.** Age-dependent fecundity and life-fertility tables for *Podisus nigrispinus* (Dallas) (Het., Pentatomidae). *J. Appl. Entomol.* 124: 319-324.
- Medeiros, R.S., F.S. Ramalho, J.C. Zanuncio & J.E. Serrão. 2003.** Effect of temperature on life table parameters of *Podisus nigrispinus* (Het., Pentatomidae) fed with *Alabama argillacea* (Lep., Noctuidae) larvae. *J. Appl. Entomol.* 127: 209-213.
- Medeiros, R.S., W.P. Lemos & F.S. Ramalho. 1998.** Efeitos da temperatura no desenvolvimento de *Podisus nigrispinus* (Dallas) (Heteroptera, Pentatomidae), predador do curuquerê-do-algodoeiro (Lepidoptera, Noctuidae). *Rev. Bras. Entomol.* 42: 121-130.
- Michel, B. 1994.** Entomofauna de los algodonales paraguayos: Hemiptera Heteroptera. Asuncion, Ministerio de Agricultura y Ganadería, 132p.
- Morales-Ramos, J.A. & J.R. Cate. 1993.** Temperature-dependent rates of *Catolaccus grandis* (Hymenoptera: Pteromalidae). *Environ. Entomol.* 22: 226-233.
- Orr, C.J. & J.J. Obrycki. 1990.** Thermal and dietary requirements for development of *Hippodamia parenthesis* (Coleoptera: Coccinellidae). *Environ. Entomol.* 19: 1523-1527.
- Panizzi, A.R., B.S. Corrêa, D.L. Gazzoni, E.B. Oliveira, G.G. Newman & S.B. Turnipseed. 1977.** Insetos da soja no Brasil. Londrina, Embrapa Soja, 20p. (Boletim Técnico).
- Santos, T.M., E.N. Silva & F.S. Ramalho. 1995.** Desenvolvimento ninfal de *Podisus connexivus* Bergroth (Hemiptera: Pentatomidae) alimentado com curuquerê-do-algodoeiro. *Pesq. Agrop. Bras.* 30: 163-167.
- Santos, T.M., E.N. Silva & F.S. Ramalho. 1996.** Consumo alimentar e desenvolvimento de *Podisus nigrispinus* (Dallas) sobre *Alabama argillacea* (Huebner) em condições de laboratório. *Pesq. Agrop. Bras.* 31: 699-707.
- Sas Institute Inc. 2000.** SAS user's guide: statistics. Cary. 584p.
- Schoolfield, R.M., P.J.H. Sharpe & C.E. Magnuson. 1981.** Non linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *J. Theor. Biol.* 88: 719-731.
- Sharpe, P.J.H. & D.W. DeMichele. 1977.** Reaction kinetics of poikilotherm development. *J. Theor. Biol.* 64: 649-670.
- Stinner, R.E., A.P. Gutierrez & G.D. Butler Jr. 1974.** An algorithm for temperature-dependent growth rate simulation. *Can. Entomol.* 106: 519-524.
- Thomas, D.B. 1992.** Taxonomic synopsis of the Asopinae Pentatomidae (Heteroptera) of the Western Hemisphere. Lanham, Entomological Society of America, 156p.
- Torres, J.B., J.C. Zanuncio & H.N. de Oliveira. 1998.** Nymphal development and adult reproduction of the stinkbug predator *Podisus nigrispinus* (Het., Pentatomidae) under fluctuating temperatures. *J. Appl. Entomol.* 122: 509-514.
- Uvarov, B.P. 1931.** Insects and climate. *Trans. Entomol. Soc. London* 79: 1-247.
- Wagner, T.L., H. Wu, P.J.H. Sharpe, R.M. Schoolfield & R.N. Coulson. 1984.** Modeling insect development rates: a literature review and a application of a biophysical model. *Ann. Entomol. Soc. Amer.* 77: 208-225.
- Worner, S.P. 1992.** Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. *Environ. Entomol.* 21: 689-699.

Received 25/03/03. Accepted 05/02/04.