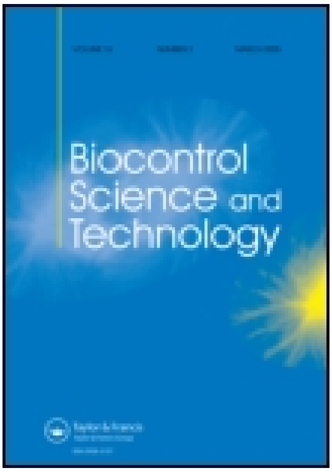

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RESEARCH ARTICLE

Modelling development of *Callosobruchus maculatus* and *Anisopteromalus calandrae* at various constant temperatures using linear and non-linear models

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The development of cowpea weevil, *Callosobruchus maculatus* (Fabricius) (Col., Bruchidae), and its parasitoid, *Anisopteromalus calandrae* (Howard) (Hym., Pteromalidae), under nine constant temperatures and the best linear and non-linear models describing the temperature-development relationships of the host and its parasitoid were determined. The pre-imaginal developmental time decreased with increasing temperature from 15° C to 35° C for both species and sexes. Based on the best-fitted linear model, the lower developmental threshold and the thermal constant were determined as 10.4° C and 526.3 degree-days for *C. maculatus* and 11.5° C and 263.2 degree-days for *A. calandrae*, respectively. Fifteen non-linear temperature-dependent models were examined to find the best model to describe the relationship between temperature and development rate of *C. maculatus* and *A. calandrae.* Among non-linear models, the Analytis model was the most efficient for the description of temperature-dependent development of *C. maculatus* and *A. calandrae.*

Keywords: cowpea weevil; *Callosobruchus maculatus*; *Anisopteromalus calandrae*; Bruchidae; Pteromalidae; thermal requirements

1. Introduction

Cowpea weevil, *Callosobruchus maculatus* (Fabricius) (Coleoptera: Bruchidae), is one of the most important stored-product pests of several pulse crops including chickpea (*Cicer arietinum* L.), cowpea (*Vigna unguiculata* (L.) Walp.), lentil (*Lens culinaris* Medik.), haricot beans (*Phaseolus vulgaris* L.) and soya (*Glycine max* Mer.). *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae) is a wasp that parasitises the larval and pupal stages of numerous coleopteran pests in stored pulses and cereals (Ghani & Sweetman, 1955; Williams & Floyd, 1971).

Information on the performance of natural enemies at various temperature regimes could be useful to select the best-adapted natural enemies to the environmental conditions of target pests (Jervis & Copland, 1996; Obrycki & Tauber, 1978). In this regard, numerous linear and non-linear models have been introduced to simulate the relationship between insect development and temperature (Briere,

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Pracros, Roux, & Pierre, 1999; Campbell, Frazer, Gilbert, Gutierrez, & Mackauer, 1974; Lactin, Holliday, Johnson, & Craigen, 1995; Logan, Wolkind, Hoyt, & Tanigoshi, 1976; Sharpe & DeMichele 1977; Stinner, Gutierrez, & Butler, 1974). By the linear regression model, researchers are able to easily calculate two constants: the lower developmental threshold (T_0) and the thermal constant (K), within a limited temperature range. However, the relationship between the development rate of insects and temperature has an asymmetrical dome-shape pattern (Campbell et al., 1974) and cannot be precisely predicted using the linear models for a wide range of temperatures. The non-linear models describe the developmental rate over a wider range of temperatures and provide the estimates of the lower and upper developmental thresholds (T_0 and T_{max}) and optimum temperature (T_{opt}) for insect development. The weakness of the non-linear approach is that estimation of thermal constant cannot be directly achieved and some models cannot estimate T_0 (Jarošík, Honek, & Dixon, 2002; Kontodimas, Eliopoulos, Stathas, & Economou 2004).

The development of *C. maculatus* and its parasitoid, *A. calandrae*, was studied at various constant temperatures. The developmental thresholds of the host and parasitoid were estimated by 2 linear and 15 non-linear temperature-dependent models. The models were then evaluated using their goodness-of-fit and the accuracy on thresholds estimation.

2. Materials and methods

2.1. Insect rearing

The cowpea weevil and its parasitoid, *A. calandrae*, were originally collected from stored products in Esfahan, Iran, in April 2010. *C. maculatus* was reared on chickpea and the parasitoid on the weevil at 28 ± 2° C,relative humidity of 55 ± 5% and a photoperiod of 12L:12D h in the laboratory for at least two generations (3 months) before being used in experiments.

2.2. The host–parasitoid development at constant temperatures

The development of *C. maculatus* and *A. calandrae* was studied at nine constant temperatures (12, 15, 20, 25, 27, 30, 35, 37 and 40° C), 55 ± 5% R.H. and a photoperiod of 12L:12D h. To start the experiments, 10 mated 1–2-day-old *C. maculatus* females were introduced into cylindrical containers (10 cm diameter × 30 cm) containing 300 chickpea seeds. The beetles were removed after 24 h, and the seeds were kept in a growth chamber with above-mentioned constant conditions. Observations were made every 24 h for monitoring the emergence of adult beetles. In this experiment, the development of at least 100 insects was investigated separately at each constant temperature.

To study the development of *A. calandrae*, 10 mated 1 –2-day-old female wasps were introduced into the cylindrical containers containing at least 100 chickpea seeds infested by the last-instar larvae of *C. maculatus*. The wasps were removed after 24 h, and the exposed hosts were placed separately into Petri dishes (7 cm diameter) and then transferred into growth chambers with above-mentioned constant conditions. Observations were made every 24 h for monitoring the emergence of adult wasps. The development of at least 50 wasps was studied at each constant temperature.

2.3. Temperature-dependent models

Two linear and 15 non-linear models were examined to find the best-fitted model to describe the effect of temperature on the development of *C. maculatus* and *A. calandrae* (Table 1). The accuracy of the models was evaluated based on both statistically goodness-of-fit and biological interpretation. The coefficient of determination (R^2) and the residual sum of squares (RSS) are well-known statistical criteria for the evaluation of goodness-of-fit of regression models. In addition, we used the corrected Akaike information criterion ($AICc$), which is parameter independent and appropriate for the discrimination of the models with different number of parameters (Hurvich & Tsai , 1993). $AICc$ is defined as:

Table 1. Linear and non-linear models to simulate the developmental rates of *C. maculatus* and *A. calandrae* at various constant temperatures.

Equation	Model	Reference
$Y = a + bX$ $T_0 = -\frac{a}{b}$ $k = -\frac{1}{b}$	Ordinary linear regression	Campbell et al. (1974) Roy et al. (2002)
$DT = k + tD$	Ikemoto & Takai	Ikemoto and Takai (2000)
$R(T) = \frac{c}{1+e^{(a-bT)}}$	Sigmoid	Analytis (1981)
$R(T) = \Psi \times \left[e^{\rho \times T} - e^{\left(\rho \times T_{\max} - \frac{T_{\max}-T}{\Delta T}\right)}\right]$	Logan 6	Logan et al. (1976)
$R(T) = a \times \left[\frac{1}{1+k \times e^{-\rho \times T}} - e^{\left(\frac{T_{\max}-T}{\Delta T}\right)}\right]$	Logan 10	Logan et al. (1976)
$R(T) = e^{\rho \times T} - e^{\left(\rho \times T_{\max} - \left(\frac{T_{\max}-T}{\Delta T}\right)\right)}$	Lactin 1	Lactin et al. (1995)
$R(T) = e^{\rho \times T} - e^{\left(\rho \times T_{\max} - \left(\frac{T_{\max}-T}{\Delta T}\right)\right)} + \lambda$	Lactin 2	Lactin et al. (1995)
$R(T) = a \times T(T - T_0) \times \sqrt{T_{\max} - T}$	Briere 1	Briere et al. (1999)
$R(T) = a \times T(T - T_0) \times \sqrt[m]{T_{\max} - T}$	Briere 2	Briere et al. (1999)
$R(T) = a \times (T - T_0)^n \times (T_{\max} - T)^m$	Analytis	Analytis (1981)
$R(T) = ax^3 + bx^2 + cx + d$	Polynomial 3rd order	Harcourt and Yee (1982)
$R(T) = a \times (T - T_0)^2 (T_{\max} - T)$	Kontodimas 16	Kontodimas et al. (2004)
$D(T) = \frac{2}{D_{min}\left(e^{k(T-T_{opt})} + e^{-\lambda(T-T_{opt})}\right)}$	Janisch	Janisch (1932)
$D(T) = R_m e^{\left(-0.5 \times \left(\frac{T-T_m}{T_\sigma}\right)^2\right)}$	Taylor	Taylor (1982)
$R(T) = \frac{c}{1+e^{a+b \times T}}$ for $T \leq T_{opt}$ $R(T) = \frac{c}{1+e^{a+b(2 \times T_{opt}-T)}}$ for $T > T_{opt}$	Stinner	Stinner et al. (1974)
$R(T) = \Psi\left[\frac{(T-T_0)^2}{(T-T_0)^2+D^2} - e^{\left(-\frac{T_{\max}-(T-T_0)}{\Delta}\right)}\right]$	Hilbert & Logan or Hilbert type III	Hilbert and Logan (1983)
$R(T) = R_m \times exp\left[-0.5\left(\frac{T-T_{opt}}{T_0}\right)^2\right]$ for $T \leq T_{opt}$ $R(T) = R_m \times exp\left[-0.5\left(\frac{T-T_{opt}}{T_{\max}}\right)^2\right]$ for $T > T_{opt}$	Lamb	Lamb (1992)

$$AIC_c = \mathrm{n}ln\left(\frac{SSE}{\mathrm{n}}\right) + 2P + \frac{2P(P+1)}{n-P-1}$$

where, n is the number of observations and p is the number of model parameters including the intercept and SSE is the sum of squares of error. The smaller the value of $AICc$ the better the fitness (Akaike, 1974). The accuracy of biological parameters (including T_0, $T_{\max}$ and K) estimated by the models was assessed by comparison with the experimentally obtained data.

2.4. Statistical analysis

For statistical analysis, each mean value is given with its standard error (SEM). Since temperature is a continuous independent variable, a linear regression method was used to fit the relationship between the dependent variable Y (developmental time) and the independent variable X (temperature). A student's t-test was used to compare the developmental times of males and females within each temperature. The observed sex ratio of parasitoid offspring was compared with the expected sex ratio of 1:1 by chi-square test. All statistical analyses were performed in SPSS 16.0 software. In ordinary linear regression and Ikemoto and Takai linear models, the data points at both ends of temperature ranges, which deviated from the straight line, were omitted in order to calculate the parameters T_0 and K correctly (Ikemoto & Takai, 2000). The analysis of all models was carried out with the Gauss–Newton algorithm using the JMP 8.0.2 (SAS Institute, 2009) statistical programme.

3. Results

3.1. Development time

C. maculatus and *A. calandrae* successfully developed to adulthood from 15° C to 37° C. No development was observed at 12° C and 40° C in both species (Table 2). When exposed to a range of temperatures, the rate of development was positively correlated with temperature in the range of 15–35° C; 37° C showed negative effects on development except for males of *A. calandrae* where increasing development rate continued until 37° C. At 35° C, the shortest mean time needed for *C. maculatus* and *A. calandrae* to complete their development were 23 and 11.6 days, respectively. The development time at each temperature was not significantly different between males and females for both species (t-test, $P > 0.05$); therefore, the data between the sexes were pooled and used for simulation (Table 2). Among the examined temperatures, 35° C was observed as the optimum temperature for the development of *C. maculatus* and *A. calandrae*. There was no significant difference between the sex ratio of *A. calandrae* progeny and the expected ratio of 1:1 at 15 and 20° C (χ^2 test). However, the ratio of female to male was significantly affected by temperature within the range of 25–37° C. When *A. calandrae* were reared at temperatures between 25° C and 37° C, the sex ratio of its offspring was more male-biased.

3.2. Model evaluation

The values of parameter estimation by various linear and non-linear models for the developmental rate of *C. maculatus* and *A. calandrae* at different temperatures are

Table 2. Mean developmental time (d ± SE) of *C. maculatus* and *A. calandrae* at seven constant temperatures.

	C. maculatus			*A. calandrae*		
Temperature (°C)	Male	Female	Pooled (male + female)	Male	Female	Pooled (male + female)
15	150.00 ± 1.00	153.33 ± 0.83	151.66 ± 1.66	126.25 ± 1.18	130.00 ± 0.40	128.12 ± 1.87
20	58.91 ± 0.30	58.65 ± 0.14	58.78 ± 0.13	34.80 ± 1.15	40.40 ± 0.60	37.60 ± 2.80
25	33.51 ± 0.25	33.88 ± 0.21	33.69 ± 0.18	18.82 ± 0.26	20.47 ± 0.37	19.64 ± 0.82
27	31.13 ± 0.17	31.27 ± 0.13	31.20 ± 0.07	15.74 ± 0.24	17.13 ± 0.24	16.43 ± 0.69
30	25.72 ± 0.15	26.62 ± 0.16	26.17 ± 0.45	14.00 ± 0.50	14.63 ± 0.52	14.31 ± 0.31
35	22.68 ± 0.36	23.26 ± 0.13	22.97 ± 0.29	11.27 ± 0.38	12.00 ± 0.63	11.63 ± 0.36
37	24.90 ± 0.53	25.20 ± 0.60	25.05 ± 0.15	11.20 ± 0.64	13.33 ± 1.60	12.26 ± 1.06

depicted in Tables 3 and 4. The R^2 value ranged from 0.92 to 0.98 and 0.88 to 0.99 for *C. maculatus* and *A. calandrae*, respectively (Table 3).

The lower developmental thresholds (T_0) for *C. maculatus* and *A. calandrae* (estimated from ordinary linear regression) were 10.4 and 11.6° C, respectively. The required degree-days for development (K) were 526 and 263 for *C. maculatus* and *A. calandrae*, respectively. The values estimated for T_0 and K by the next linear model, Ikemoto and Takai, were notably different than those estimated by ordinary linear model (Table 4). Both linear models do not provide the estimation for both the optimal (T_{opt}) and upper temperature thresholds (T_{max}). Among non-linear models, the lowest values of RSS and AIC_c for *C. maculatus* were estimated by the Lamb and Sigmoid models. Hilbert and Logan, Briere 1 and Kontodimas 16 provided the similar trend for *A. calandrae*. The fitted curves by the linear and non-linear models for the description of relationships between development and temperature for both species are presented in Figures 1 and 2. The Sigmoid, Logan 6, Logan 10, Lactin 1, Janisch, Stinner and Taylor models did not estimate the lower temperature threshold (Table 4). In contrast, the Briere 1, Briere 2, Hilbert and Logan, Analytis and Kontodimas models provided estimates for lower and upper temperature thresholds and optimal temperature. T_0 values were estimated as 10.4, 10.4, 4.21, 12.8 and 8.3° C for *C. maculatus* by the Briere 1, Briere 2, Hilbert and Logan, Analytis and Kontodimas models, respectively; these values for *A. calandrae* were 12.3, 12.7, 3.46, 12.8, and 9.8° C, respectively. Also, T_0 estimated graphically using Lactin 2, third-order polynomial and Lamb as 12.44, 10.51 and 4.40° C for *C. maculatus*, and as 13.49, 12.36 and 6.97° C for *A. calandrae*, respectively (Figures 1 and 2). The optimum temperature for development (T_{opt}) was estimated by all non-linear models except Sigmoid model (Table 4).

4. Discussion

Although little is known about the performance of *A. calandrae* under various constant temperatures, Lale and Vidal (2003) demonstrated an adverse effect of temperature and total developmental times of *C. maculatus* and *Callosobruchus subinnotatus* (Pic). They also introduced 35° C as the optimum temperature for the development of *C. maculatus*; the fact that is supported by the present study. Loganathan, Jayas, Fields, and White (2011) found 0° C and 42° C as the low and high temperatures for the control of *C. maculatus*. In the present study, on the contrary, no development was observed at 12° C and 40° C; this indicates that various populations of *C. maculatus* may have different vulnerability to low and high extreme temperatures. The pre-imaginal developmental time estimated for male and female *A. calandrae* at 25° C was reported by Kazemi, Talebi, and Fathipour (2008) as 18.2 and 19.8 days, respectively, which is in agreement with our data at the same temperature.

When two linear models were compared using R^2 values, Ikemoto and Takai indicated better fit for both *C. maculatus* and *A. calandrae* compared with ordinary linear regression. Meanwhile, since no development was observed at 12° C in the laboratory for *A. calandrae* and *C. maculatus*, certainly the real lower developmental threshold should be between 12° C and 15° C; therefore, the T_0 values estimated by Ikemoto and Takai model are more reliable than the linear model that predicted values <12° C. The developmental rate–temperature relationship for the insects and

Table 3. Evaluation of different models to simulate the effect of temperature on the development of *C. maculatus* and *Anisopteromalus calandrae.*

		C. maculatus			*A. calandrae*		
Model	Number of parameters	R^2	*RSS*	*AICc*	R^2	*RSS*	*AICc*
Linear regression	2	0.9248	0.00500	−63.6782	0.8783	0.00771	−55.5622
Ikemoto	2	0.9788	994322.63	55.2845	0.9936	111379.66	88.8112
sigmoid	3	0.9637	0.00241	−77.3071	0.9010	0.00627	−59.4228
Logan 6	4	0.9567	0.00288	−73.5255	0.8832	0.00740	−55.9315
Logan 10	5	0.9669	0.00220	−63.8096	0.9016	0.00623	−55.4804
Lactin 1	3	0.9567	0.00288	−66.0886	0.8832	0.00740	−57.9315
Lactin 2	4	0.9673	0.00217	−65.9389	0.9029	0.00615	−57.5967
Briere 1	3	0.9666	0.00222	−67.9389	0.9030	0.00615	−59.5967
Briere 2	4	0.9666	0.00222	−65.9552	0.9031	0.00614	−57.6114
Analytis	5	0.9680	0.00213	−63.9878	0.9035	0.00612	−55.6408
Polynomial 3rd order	4	0.9661	0.00225	−65.9552	0.9031	0.00614	−57.5967
Stinner	4	0.9637	0.00241	−65.7456	0.9010	0.00627	−57.4228
Lamb	4	0.9687	0.00208	−64.7160	0.8904	0.00659	−56.4961
Janisch	4	0.9639	0.00240	−65.8741	0.9032	0.00619	−57.5348
Taylor	3	0.9645	0.00236	−67.5092	0.8988	0.00642	−59.2101
Kontodimas 16	3	0.9661	0.00225	−67.9389	0.9030	0.00615	−59.5967
Hilbert and Logan	5	0.9684	0.00210	−64.1194	0.9047	0.00604	−55.7592

Table 4. Parameters estimated by the different models to simulate the total developmental rate of *C. maculatus* and *A. calandrae* at various constant temperatures.

Model	Parameters	*C. maculatus*	*A. calandrae*
Linear regression	a	−0.0196 ± 0.0005	−0.0439 ± 0.0030
	b	0.0019 ± 0.0000	0.0038 ± 0.0001
	K	526.3157 ± 7.6497	263.2128 ± 7.6497
	T_0	10.4224 ± 0.1809	11.5460 ± 0.4750
Ikemoto & Takai	K	475.5550 ± 3.1776	235.8806 ± 2.7720
	T	12.0015 ± 0.0685	13.2129 ± 0.0828
Sigmoid or Logistic	a	4.8558 ± 0.0765	5.4355 ± 0.3363
	b	0.2169 ± 0.0040	−0.2259 ± 0.0149
	K	0.0450 ± 0.0004	0.0925 ± 0.0023
Logan 6	ψ	−0.9817 ± 55.4453	0.1873 ± 5.4920
	p	0.1456 ± 0.0000	0.1504 ± 0.0000
	T_{max}	41.0138 ± 0.1195	41.5037 ± 0.4869
	T_{opt}	34.14	34.87
	Δ	6.8710 ± 0.1213	6.6308 ± 0.4897
Logan 10	a	0.0470 ± 0.0005	0.0942 ± 0.0029
	p	0.2032 ± 0.0040	0.2202 ± 0.0156
	T_{max}	37.0562 ± 0.0028	37.0823 ± 0.0236
	T_{opt}	36.86	36.89
	Δ	0.0235 ± 0.0000	0.0235 ± 0.0000
	k	104.2863 ± 7.5053	207.8511 ± 70.9441
Lactin 1	p	0.1455 ± 0.0013	0.1505 ± 0.0055
	T_{max}	41.0139 ± 0.1195	41.5029 ± 0.4864
	Δ	6.8689 ± 0.0606	6.6372 ± 0.2446
	T_{opt}	34.14	34.87
Lactin 2	p	0.0022 ± 0.0000	0.0041 ± 0.0002
	T_{max}	51.9172 ± 1.4030	50.8374 ± 5.070
	T_{opt}	34.60	35.94
	Δ	3.5331 ± 0.3552	3.4716 ± 1.3494
	λ	−1.0278 ± 0.0008	−1.0581 ± 0.0052
Briere 1	a	0.0000 ± 0.0000	0.0000 ± 0.0000
	T_0	10.3806 ± 0.1784	12.3394 ± 0.6571
	T_{max}	41.9080 ± 0.1721	43.0290 ± 0.7061
	T_{opt}	34.75	36.12
Briere 2	a	0.0000 ± 0.0000	0.0000 ± 0.0000
	m	1.9840 ± 0.2519	1.5111 ± 0.8041
	T_0	10.4019 ± 0.3863	12.7170 ± 0.8794
	T_{max}	41.9709 ± 0.0126	46.3979 ± 6.9414
	T_{opt}	34.79	36.77
Analytis	a	0.0016 ± 0.0004	0.0017 ± 0.0021
	n	1.1981 ± 0.2901	1.1981 ± 0.2901
	m	0.1219 ± 0.0223	0.1529 ± 0.1503
	T_{min}	12.8453 ± 0.5155	12.8435 ± 1.4530
	T_{max}	38.8481 ± 2.6554	38.8481 ± 2.6554
	T_{opt}	35.05	35.91

Table 4 (*Continued*)

Model	Parameters	*C. maculatus*	*A. calandrae*
Polynomial third order	a	0.0000 ± 0.0000	0.0000 ± 0.0000
	b	0.0003 ± 0.0000	0.0005 ± 0.0002
	c	−0.0033 ± 0.0009	−0.0074 ± 0.0050
	d	0.0104 ± 0.0078	0.0284 ± 0.0403
	T_{opt}	35.48	37.34
	T_{max}	49.10	51.44
Stinner	a	4.8558 ± 0.0765	5.4356 ± 0.3363
	b	−0.2169 ± 0.0040	−0.2259 ± 0.0149
	c	0.0450 ± 0.0004	0.0926 ± 0.0023
	T_{opt}	35.4330 ± 0.3542	36.0899 ± 0.8170
Lamb	R_m	0.0431 ± 0.0002	0.0954 ± 0.0013
	T_m	35.4677 ± 0.1595	35.9455 ± 0.5636
	T_L	11.2950 ± 0.0388	9.5958 ± 0.1097
	T_H	4.1783 ± 0.5349	−2.3199 ± 0.2761
	T_{opt}	34.90	35.95
Janisch	D_{min}	38.8609 ± 2.6472	29.0430 ± 4.6750
	k	0.0091 ± 0.0050	−0.0183 ± 0.0091
	T_{opt}	23.7965 ± 0.7752	21.6713 ± 1.1569
	λ	0.1955 ± 0.0106	0.2844 ± 0.0431
Taylor	R_m	0.0424 ± 0.0002	0.0867 ± 0.0013
	T_m	34.9083 ± 0.1604	35.9087 ± 0.5641
	T_δ	10.9772 ± 0.1207	10.5341 ± 0.4916
	T_{opt}	34.95	35.91
Kontodimas 16	a	0.0000 ± 0.0000	9.8522 ± 0.6673
	T_0	8.2661 ± 0.1517	9.8522 ± 0.6673
	T_{max}	48.9313 ± 0.3324	50.5165 ± 0.3810
	T_{opt}	35.34	36.96
Hilbert and Logan	ψ	0.0675 ± 0.0027	0.7021 ± 0.0069
	T_0	4.2142 ± 0.2048	3.4617 ± 0.8858
	D	18.1696 ± 0.0600	77.3929 ± 2.8959
	T_{max}	41.4865 ± 0.2885	39.1580 ± 1.0613
	Δ	1.1758 ± 0.2525	1.7520 ± 0.0471
	T_{opt}	34.32	35.09

mites is typically curvilinear (Briere & Pracros, 1998). Clearly, the linear models are not able to simulate this relationship across the entire curve, and the estimated value for T_0 is indeed the result of extrapolation of the regression beyond the linear portion of the curve. Nevertheless, the linear models have been widely used by the researchers for their simplicity and ability in the calculation of thermal constant (K).

The curvilinear relationship can be adequately described by several non-linear rate models; however, usually only one or two of these are retained in each case based on goodness-of-fit and estimable temperature-related biological parameters (Roy, Brodeur, & Cloutier, 2002). Most of the non-linear models used in this study showed highly statistical goodness-of-fit according to R^2, *RSS* and *AICc* values. Therefore, the temperature-related biological parameters (T_0, T_{opt} and T_{max}) were used to select the best model for describing the relationship between developmental

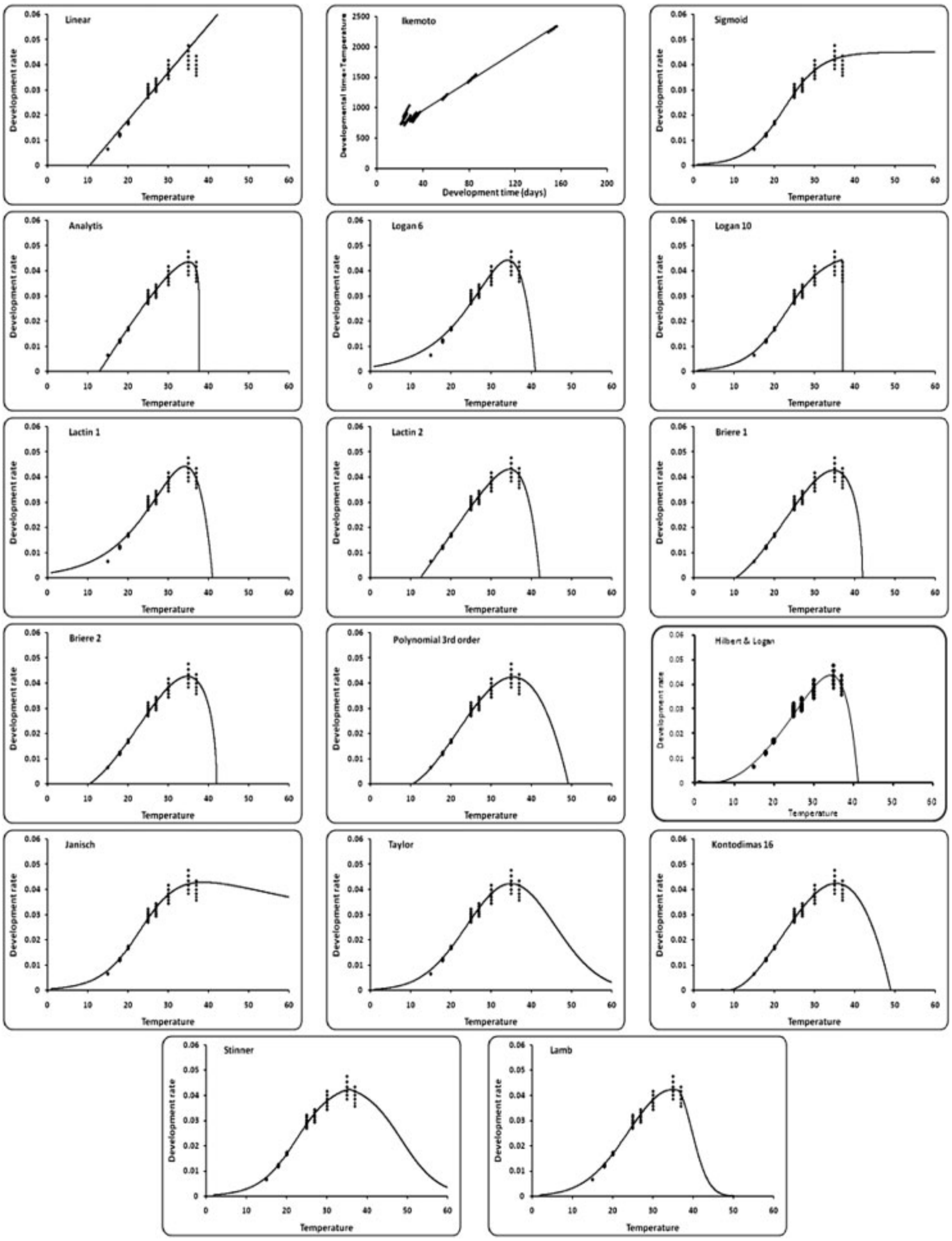

Figure 1. Observed (dots) and predicted (lines) developmental rates of *C. maculatus* by different models.

rates of *C. maculatus* and *A. calandrae* and temperature. The Sigmoid, Logan 6, Logan 10, Lactin 1, Janisch, Stinner and Lamb models did not estimate T_0 because there was no intersection with the temperature axis (Figures 1 and 2). Based on the experimental data, the real values for T_{opt} and T_{max} for both species should be between 35–37° C and 37–40° C, respectively (Table 2). Lactin 2, third-order

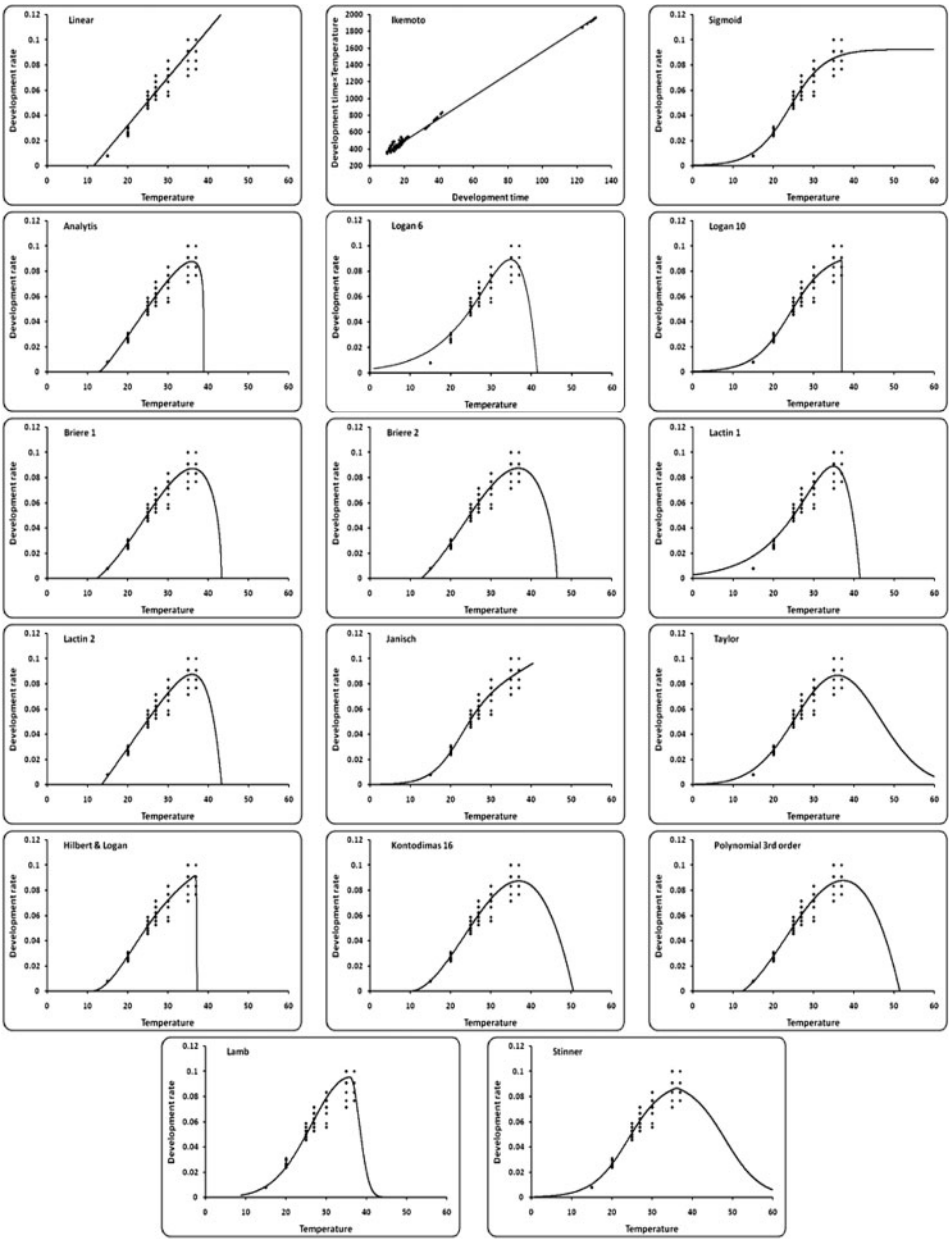

Figure 2. Observed (dots) and predicted (lines) developmental rates of *A. calandrae* by different models.

polynomial, Briere 1, Briere 2, Kontodimas 16 and Hilbert and Logan models clearly overestimated $T_{\max}$ for both species. In contrast, the Lamb and Taylor models underestimated $T_{\max}$. The estimated T_{opt} by the Janisch model was lower than the experimental values for both species. Between all the non-linear models, the Analytis model was the most efficient for the description of temperature-dependent development of the pest and its parasitoid; it estimated the values of T_0, T_{opt} and T_{max} very well, which were in accordance with experimental data.

An important factor influencing success or failure of parasitoids is the offspring sex ratio (Waage & Hassell, 1982), which is affected by various factors, such as host plant, food quality, temperature and photoperiod (Deng & Tsai, 1998). The higher ratio of female offspring is more favourable for increasing the success of biological control programmes by parasitoids. The findings of the present study showed that more female progeny of *A. calandrae* were obtained at 15, 20 and 27° C compared with other temperatures; the ratio of females severely declined near the upper extreme temperatures (35° C and 37° C).

In conclusion, the present study provides realistic information on the effect of a broad range of temperatures on the development of *C. maculatus* and *A. calandrae*. The Analytis model was recognised as the best model for the simulating development of *C. maculatus* and *A. calandrae* at various temperatures. *A. calandrae* could be considered as an efficient candidate for the biological control of cowpea weevil only at a narrow range of intermediate temperatures (25 and 27° C). This is not a reason for the inefficiency of *A. calandrae*, since the storage temperature can be adjusted to a desired range. Further studies are needed to determine the effect of other environmental factors such as humidity, photoperiod and host quality on the development and performance of *A. calandrae.*

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