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# A Novel Rate Model of Temperature-Dependent Development for Arthropods

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**ABSTRACT** Two novel and simple mathematical models of arthropod temperature-dependent development are proposed. These models are easy to use and have 3 (equation 1) and 4 (equation 2) ecologically meaningful parameters, respectively. Each parameter can be estimated using nonlinear regression. These models were used to compare developmental rates at constant temperatures for our own experiments on *Lobesia botrana* (Dennis & Schiffermuller) and for data from 6 insect species described (a total of 13 stages). In all cases, we obtained an accurate nonlinear description of the rate of development against temperature given by the adjusted  $R^2$  (Kvalseth, 1985). The adjusted  $R^2$  calculated extended from 0.86 to 0.99 and were identical for our equations 1 and 2. In all cases, equation 2 provided the lowest residual sums of squares. The models gave upper  $T_L$  and lower  $T_0$  temperature threshold estimations, and the estimations obtained were better by using equation 1 rather equation 2. Confidence intervals for each parameter were given and a comparison between estimated and observed temperature thresholds were presented.

**KEY WORDS** temperature, developmental rate, model, insect, arthropod

TEMPERATURE IS ONE of the most important factors that influences the developmental rate of arthropods. Among insects and mites, the relationship of developmental rate to constant temperature tends to be nonlinear for arthropods. Development does not occur below a low-temperature threshold; above this the rate increases with temperature until an optimum is reached; at supra-optimal temperatures the rate decreases rapidly to zero at the upper lethal limit. The rate curve accelerates at temperatures near the lower threshold increases constantly at intermediate temperatures and decelerates as temperatures approach the optimum.

Numerous studies determined an appropriate developmental rate function for phenological or population models that can be used under a variety of conditions to predict important events in insect life cycles (Gutierrez et al. 1980, Croft and Knight 1983, Hudes and Shoemaker 1988), or insect abundance for control strategies (Poole 1978, Plantegenest 1995, Briere et al. 1996). The developmental rate function for each developmental stage is determined by rearing insects at range of constant temperatures. Several approaches have been used to model the developmental rates obtained. The earliest model was the linear degree-day model. It has the advantage of simplicity and

allows estimation of the developmental threshold and the degree-day requirement of insect species. However, this model does not include nonlinearity at high and low temperatures and produces biased results. Nonlinear models have been developed to improve these results. Many nonlinear models are empirical, including the simple catenary curve of Janisch (1932), the Belehradek model (1935), the logistic equation of Davidson (1942), and later the various matched asymptotic curves of Logan et al. (1976, Logan 1988). The empirical functions proposed by Logan et al. (1976) have 4 or 5 parameters with biological significance (according to the versions). They are defined by combining 2 functions with matched asymptotes, generally a sigmoid or an exponential equation and an exponential equation at low and high temperatures respectively. Lactin et al. (1995) have proposed an improved version of Logan's model by eliminating a redundant parameter. Other functions developed by Sharpe and DeMichele (1977) were based on enzyme kinetics, and all 6 parameters have a thermodynamic biochemical interpretation. In its original form, these thermodynamic parameters were found to be highly correlated, rendering nonlinear parameter estimation techniques inadequate. To eliminate this correlation, Schoolfield et al. (1981) reparametrized the Sharpe and DeMichele model to allow nonlinear estimation techniques. Although mathematically somewhat complex, the Logan models, the Sharpe and DeMichele model, and the Schoolfield model have been fitted successfully to a large number of data sets.

Our objective was to produce a simplified model of development that can describe the nonlinear relation-

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ship of developmental rate to temperature for several insect species and provide an upper and lower estimated developmental threshold. First, to reduce the number of parameters, a 3-parameter model with a nonlinear part at low and high temperatures and a linear portion at intermediate temperatures is proposed. Second, to generalize this 3-parameter model, a 2nd general model with 4 parameters is tested to determine if the additional parameter improves fit. These 2 new models were developed initially to predict the development of the grape berry moth, *Lobesia botrana* (Dennis & Schiffermüller). Briere and Pracros (1998) performed experimental studies to obtain developmental rates at constant temperatures and to compare them with 5 prevalent models in the literature. The model of Logan (1976, equation 10) gave the best results but required estimation of 5 parameters. In this article, these 2 new models were applied to several insect species to determine if development could be modeled using fewer parameters.

### Materials and Methods

**Mathematical Models.** First, to describe the temperature-dependent developmental rates of 6 species (a total of 13 data sets), we proposed the following new model,

$$R(T) = \begin{cases} 0 & T \leq T_0 \\ aT(T - T_0)\sqrt{T_L - T} & T_0 \leq T \leq T_L \\ 0 & T \geq T_L \end{cases} \quad [1]$$

where  $R$  is the rate of development and is a positive function of temperature  $T$  in degree Centigrade.  $T_L$  is the lethal temperature (upper threshold),  $T_0$  the low temperature developmental threshold (lower threshold), and  $a$  is an empirical constant.

To establish this new empirical function, 4 criteria were taken into account: (1) the possibility to determine lower and upper temperature thresholds; (2) asymmetry about the optimum temperature, the point at which the rate of development is greatest; (3) presence of an inflection point; and (4) a sharp decline in development rate at temperatures above the optimum temperature.

The lower and the upper thermal limits were explicitly included in the mathematical expression and constituted 2 parameters of the model,  $T_0$  and  $T_L$ , respectively. To obtain a sharp decline at high temperatures, we have used a square root, which permits a high slope when the temperature approaches the threshold  $T_L$ . The products of the different powers of  $T$  show a nonlinear response with an inflection point.

We subsequently propose a more general model in which the square root (equivalent to a power equal to  $1/2$ ) is replaced by a general power equal to  $1/m$ , where  $m$  is a new parameter to evaluate. This new model is composed in this case of 4 parameters:

$$R(T) = \begin{cases} 0 & T \leq T_0 \\ aT(T - T_0)(T_L - T)^{\frac{1}{m}} & T_0 \leq T \leq T_L \\ 0 & T \geq T_L \end{cases} \quad [2]$$

and the optimum temperature  $T_{opt}$  for equation 2 can be found numerically by equating  $dR(T)/dT$  to zero and taking the biggest root as the solution for  $T$ .  $T_{opt}$  is equal to

$$T_{opt} = \frac{(2mT_L + (m+1)T_0 + \sqrt{4m^2T_L^2 + (m+1)^2T_0^2 - 4m^2T_0T_L})}{4m+2} \quad [3]$$

This expression depends only on  $T_L$ ,  $T_0$ , and  $m$ .

**Data Sources.** To test the general applicability of these new models, temperature-dependent developmental rates for a variety of insects were selected from the literature. These were the grape berry moth, *L. botrana* (Dennis & Schiffermüller) (Lepidoptera: Tortricidae) (Briere and Pracros 1998); the red turnip beetle, *Entomoscelis americana* Brown (Coleoptera: Chrysomelidae) (Lamb et al. 1984); the pea aphid *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae) (Lamb 1992); 2 geographical biotypes (G and A) of *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae) (Stinner et al. 1974, Sharpe et al. 1981); the flea beetle *Aphthona abdominalis* Duftschmid (Coleoptera: Chrysomelidae) (Fornasari 1995); and the migratory grasshopper, *Melanoplus sanguinipes* (F.) (Orthoptera: Acrididae) (Hilbert and Logan 1983). Certain data were gathered. The developmental rate data were pooled for the 2 clones of *A. pisum* and the 2 biotypes of *H. zea*. Two data sources were used for *H. zea*, 1 for the egg stage (Stinner et al. 1974) and the other for larvae and pupae (Sharpe et al. 1981).

All data were expressed as developmental rates calculated as the reciprocal of development time in days (1/d). To evaluate parameter estimates, experimental values were collected for the lower and upper developmental thresholds and used to establish an optimum temperature for each stage of development. These predicted values were calculated using equation 3 and the observed optimum values were determined graphically by the data sets. For *H. zea* and *A. pisum*, the observed values for each threshold were not found and are missing in Table 2.

**Analytical Method.** We fitted the curves by iterative nonlinear regression based on the Marquardt algorithm (PROC NLS2, Splus 1988).

**Criteria of Comparison.** The number of parameters and the number of degrees of freedom change according to the model (3 or 4 parameters) and to the data set respectively, so we calculated the adjusted coefficient of determination using expression of Kvalseth (1985):

$$\hat{R}^2 = 1 - (1 - R^2) \left( \frac{n-1}{n-k-1} \right) \quad [4]$$

where  $\hat{R}^2$  is the adjusted coefficient of determination,  $n$  is the number of observations,  $k$  is the number of parameters in the  $i$ th function, and  $R^2$  is computed as

$$R^2 = 1 - \frac{\sum_{j=1}^n (y_j - \hat{y}_j)^2}{\sum_{j=1}^n (y_j - \bar{y})^2} \quad [5]$$

Table 1. Number of data points (n), parameter estimates and asymptotic standard errors for the new nonlinear models (Equations (1) and (2)) of temperature-dependent developmental rate, applied to several published data sets.

| Insect species          | Stage            | n  | Equation | Model parameters          |                             |                       |       |       |                             |      |                             |
|-------------------------|------------------|----|----------|---------------------------|-----------------------------|-----------------------|-------|-------|-----------------------------|------|-----------------------------|
|                         |                  |    |          | a<br>( $\times 10^{-4}$ ) | SEM<br>( $\times 10^{-4}$ ) | $T_0$                 | SEM   | $T_L$ | SEM<br>( $\times 10^{-1}$ ) | m    | SEM<br>( $\times 10^{-2}$ ) |
| A <i>L. botrana</i>     | egg              | 12 | 1        | 1.7                       | 0.064                       | 10.55                 | 0.467 | 34.00 | 0.081                       | 2    |                             |
|                         |                  |    | 2        | 1.57                      | 0.075                       | 11.26                 | 0.415 | 34.00 | 0.15                        | 1.75 | 9.16                        |
| B <i>L. botrana</i>     | L1               | 14 | 1        | 2                         | 15.4                        | 9.00                  | 0.885 | 34.90 | 2.64                        | 2    |                             |
|                         |                  |    | 2        | 2.34                      | 0.42                        | 8.60                  | 1.22  | 34.64 | 4.38                        | 2.31 | 0.494                       |
| C <i>L. botrana</i>     | L2               | 13 | 1        | 2.3                       | 0.15                        | 7.86                  | 0.887 | 34.60 | 1.61                        | 2    |                             |
|                         |                  |    | 2        | 2.14                      | 0.38                        | 8.33                  | 1.11  | 34.77 | 4.02                        | 1.88 | 29.7                        |
| D <i>L. botrana</i>     | L3               | 13 | 1        | 2.4                       | 0.12                        | 8.10                  | 0.704 | 34.00 | 0.072                       | 2    |                             |
|                         |                  |    | 2        | 2.47                      | 0.16                        | 7.72                  | 1.02  | 34.00 | 0.05                        | 2.10 | 19.6                        |
| E <i>L. botrana</i>     | L4               | 13 | 1        | 2.3                       | 0.15                        | 9.00                  | 0.850 | 34.00 | 0.108                       | 2    |                             |
|                         |                  |    | 2        | 2.5                       | 0.2                         | 7.70                  | 1.34  | 34.00 | 0.020                       | 2.46 | 32.3                        |
| F <i>L. botrana</i>     | L5               | 13 | 1        | 1.25                      | 0.068                       | 7.73                  | 0.805 | 34.00 | 0.153                       | 2    |                             |
|                         |                  |    | 2        | 1.28                      | 0.093                       | 7.40                  | 1.18  | 34.00 | 0.125                       | 2.00 | 21.5                        |
| G <i>L. botrana</i>     | pupae            | 13 | 1        | 0.95                      | 0.042                       | 11.55                 | 0.530 | 36.41 | 0.998                       | 2    |                             |
|                         |                  |    | 2        | 1.2                       | 0.043                       | 10.00                 | 0.543 | 36.10 | 0.366                       | 2.84 | 19.9                        |
| H <i>M. sanguinipes</i> | nymphs           | 19 | 1        | 0.19                      | 0.023                       | 15.74                 | 1.58  | 48.90 | 8.83                        | 2    |                             |
|                         |                  |    | 2        | 0.323                     | 0.11                        | 12.76                 | 5.27  | 46.64 | 1.38                        | 3.92 | 3.8                         |
| I <i>A. pisum</i>       |                  | 40 | 1        | 1.12                      | 0.084                       | $-2.1 \times 10^{-2}$ | 1.00  | 32.29 | 5.23                        | 2    |                             |
|                         |                  |    | 2        | 2                         | 0.097                       | -6.24                 | 2.38  | 28.57 | 3.22                        | 5.40 | 1.12                        |
| J <i>A. abdominalis</i> | egg              | 6  | 1        | 1.035                     | 0.11                        | 12.92                 | 1.06  | 42.14 | 8.70                        | 2    |                             |
|                         |                  |    | 2        | 2                         | 0.27                        | 11.26                 | 1.40  | 38.85 | 7.05                        | 4.50 | 1.61                        |
| K <i>H. zea</i>         | larvae and pupae | 22 | 1        | 0.211                     | 0.016                       | 11.25                 | 0.623 | 42.05 | 9.35                        | 2    |                             |
|                         |                  |    | 2        | 0.463                     | 0.040                       | 9.33                  | 1.22  | 36.80 | 8.14                        | 5.10 | 2.15                        |
| L <i>H. zea</i>         | egg              | 10 | 1        | 2.25                      | 0.16                        | 10.98                 | 0.713 | 39.93 | 6.34                        | 2    |                             |
|                         |                  |    | 2        | 3.41                      | 1.04                        | 9.98                  | 1.42  | 37.70 | 1.80                        | 2.90 | 1.20                        |
| M <i>E. americana</i>   | egg              | 15 | 1        | 5.25                      | 0.47                        | 4.63                  | 1.77  | 38.81 | 1.52                        | 2    |                             |
|                         |                  |    | 2        | 5                         | 0.75                        | 5.37                  | 2.13  | 38.90 | 3.03                        | 1.80 | 27.8                        |

where  $y_j$  is the  $j$ th observed mean developmental rate and  $\hat{y}_j$  the  $j$ th predicted developmental rate. The use of this coefficient of determination provides information about the quality of the curve representing the data and can be considered as a good criterion (Lamb et al. 1984). We have also studied the confidence intervals for each parameter estimated by equations 1 and 2 as the residuals sums of squares.

Results and Discussion

Parameter estimates from the nonlinear regressions with the asymptotic standard errors are given in Table 1. A comparison between the lower, the upper, and the optimum thresholds observed and predicted by equation 1 and 2 are given in Table 2. The confidence intervals for each parameter, the  $R^2$  values as the residual sums of squares are presented in Table 3. Table 4 enumerates the features of the most popular models and provides criteria to evaluate the performance of our new models. Plots of the fitted curves for equation 1 and data are displayed in Figs. 1 and 2. Fig. 3 represents equation 2 for various values of the parameter  $m$ .

The adjusted  $R^2$  obtained in each case (Table 2) indicated the good fit of the curves to the data. The values calculated for equations 1 and 2 were similar. The lowest value was obtained for *M. sanguinipes* (0.86) because the data used in the literature covered only the linear temperature range of the developmental rate. We have made a comparison between the magnitude of the respective residual sums of squares (RSS) for equations 1 and 2, and we have ascertained that equation 2 had a smaller RSS than equation 1.

Equation 1 is analytic over the entire temperature range and allows a representation of the asymmetry about the optimum temperature. This nonlinear description of the developmental rate is necessary to provide an adequate ecological description (Hilbert and Logan 1983). Moreover, the developmental rate curve intercepts the temperature axis at high and low temperatures, allowing estimation of an upper and lower developmental threshold. For data covering the entire temperature range, equation 1 gives correct values for each developmental threshold (Table 2). Only for 3 larval stages of *L. botrana* (2nd, 3rd, and 5th) were the lower thresholds not predicted precisely. Differences between 1.1°C and 2.6°C were obtained (Table 2). Although for all stages, lethal and optimum predicted temperatures were similar to lethal and optimum observed temperatures, the estimated values of the maximum rate are nevertheless a little lower than the experimental values. This is the case for *A. pisum*, *E. americana* egg stage, and the 1st, 2nd, 3rd, and 4th larval stages of *L. botrana*.

The estimated values of  $T_0$  and  $T_L$  were more closely predicted using equation 1 compared with equation 2 (Table 2). Compared with the estimated values given by equation 1, equation 2 gives upper thresholds  $T_L$  that are lower by 2.2, 2.4, 3.3, 3.7, and 5.4°C for *H. zea* (egg), *M. sanguinipes*, *A. abdominalis*, *A. pisum*, and *H. zea* (egg to adult). Predicted lethal temperatures values were similar to observed values for *E. americana* and all stages of *L. botrana*. The  $T_L$  confidence intervals for equations 1 and 2 have similar bounds.

The differences calculated for the threshold temperature  $T_0$  by equations 1 and 2 were not as great as for  $T_L$  and the values predicted by equation 2 were also

**Table 2.** Comparison between observed and estimated values using equations (1) and (2) for the lower ( $T_0$ ), the upper ( $T_L$ ) and the optimum temperature ( $T_{opt}$ ) thresholds (expressed in °C) of different insect species.

| Insect species          | Stage        | Equation | $T_0$     |                 | $T_L$     |          | $T_{opt}$ |                     |
|-------------------------|--------------|----------|-----------|-----------------|-----------|----------|-----------|---------------------|
|                         |              |          | Estimated | Observed        | Estimated | Observed | Estimated | Observed            |
| A <i>L. botrana</i>     | egg          | 1        | 10.55     | 10              | 34.00     | 34       | 28.50     | 28                  |
|                         |              | 2        | 11.26     |                 | 34.00     |          | 28.00     |                     |
| B <i>L. botrana</i>     | L1           | 1        | 9.00      | 9               | 34.90     | 34       | 29.00     | 28 < $T_{Opt}$ < 30 |
|                         |              | 2        | 8.60      |                 | 34.64     |          | 29.38     |                     |
| C <i>L. botrana</i>     | L2           | 1        | 7.86      | 9               | 34.60     | 34       | 28.60     | 28 < $T_{Opt}$ < 30 |
|                         |              | 2        | 8.33      |                 | 34.77     |          | 28.35     |                     |
| D <i>L. botrana</i>     | L3           | 1        | 8.10      | 10              | 34.00     | 34       | 28.10     | 28 < $T_{Opt}$ < 30 |
|                         |              | 2        | 7.72      |                 | 34.00     |          | 28.33     |                     |
| E <i>L. botrana</i>     | L4           | 1        | 9.00      | 10              | 34.00     | 34       | 28.30     | 28 < $T_{Opt}$ < 30 |
|                         |              | 2        | 7.70      |                 | 34.00     |          | 29.00     |                     |
| F <i>L. botrana</i>     | L5           | 1        | 7.73      | 10              | 34.00     | 34       | 28.00     | 28 < $T_{Opt}$ < 30 |
|                         |              | 2        | 7.40      |                 | 34.00     |          | 28.30     |                     |
| G <i>L. botrana</i>     | pupae        | 1        | 11.55     | 12              | 36.41     | 36       | 30.55     | 28 < $T_{Opt}$ < 30 |
|                         |              | 2        | 10.00     |                 | 36.10     |          | 31.60     |                     |
| H <i>M. sanguinipes</i> | nymphs       | 1        | 15.74     | 17.8/22         | 48.90     | 49       | 41.07     | 39 < $T_{Opt}$ < 41 |
|                         |              | 2        | 12.76     |                 | 46.64     |          | 42.20     |                     |
| I <i>A. pisum</i>       |              | 1        | -0.02     | —               | 32.29     | —        | 25.83     | 25 < $T_{Opt}$ < 26 |
|                         |              | 2        | -6.24     |                 | 28.57     |          | 25.92     |                     |
| J <i>A. abdominalis</i> | egg          | 1        | 12.92     | 12 < $T_0$ < 13 | 42.14     | 41       | 35.29     | 35 < $T_{Opt}$ < 36 |
|                         |              | 2        | 11.26     |                 | 38.85     |          | 35.63     |                     |
| K <i>H. zea</i>         | egg to adult | 1        | 11.25     | —               | 42.05     | —        | 34.98     | 34 < $T_{Opt}$ < 35 |
|                         |              | 2        | 9.33      |                 | 36.80     |          | 33.84     |                     |
| L <i>H. zea</i>         | egg          | 1        | 10.98     | —               | 39.93     | —        | 33.26     | 32 < $T_{Opt}$ < 35 |
|                         |              | 2        | 9.98      |                 | 37.70     |          | 33.00     |                     |
| M <i>E. americana</i>   | egg          | 1        | 4.63      | 5               | 38.81     | 38.5     | 31.55     | 32 < $T_{Opt}$ < 33 |
|                         |              | 2        | 5.37      |                 | 38.90     |          | 31.30     |                     |

lower than these predicted by equation 1 (Table 2). We obtained differences within 0–1°C for 1st, 2nd, 3rd, and 5th *L. botrana* stages and *E. americana* stage; 1–2°C for the 4th and pupae stages of *L. botrana*, *H. zea* (egg and egg to adult stage), and *A. abdominalis*; equal to 3°C for *M. sanguinipes* and equal to 6.2°C for *A.*

*pisum*. The  $T_0$  confidence intervals for equations 1 and 2 have different bounds and the  $T_0$  confidence intervals for equation 2 are larger than for equation 1.

There was not a very large difference between the optimum temperatures estimated by equations 3 and the observed optimum temperature (Table 2). The

**Table 3.** Confidence intervals (lower and upper bounds) for parameters a,  $T_0$ ,  $T_L$  and m,  $R^2$  values and residuals sums of squares for equations (1) and (2).

| Insect species          | Stage            | Equation | Confidence Intervals   |                     |                    |                   | $R^2$ | SSR<br>( $\times 10^{-5}$ ) |
|-------------------------|------------------|----------|------------------------|---------------------|--------------------|-------------------|-------|-----------------------------|
|                         |                  |          | a ( $\times 10^{-4}$ ) | $T_0$               | $T_L$              | m                 |       |                             |
| A <i>L. botrana</i>     | egg              | 1        | [1.5810; 1.8310]       | [9.6401; 11.4727]   | [33.9888; 34.0209] | —                 | 0.98  | 6.2936                      |
|                         |                  | 2        | [1.4231; 1.7173]       | [10.4531; 12.0824]  | [33.9827; 34.0418] | [1.5716; 1.9308]  | 0.98  | 4.2486                      |
| B <i>L. botrana</i>     | L1               | 1        | [1.7506; 2.3545]       | [7.3312; 10.8014]   | [34.4443; 35.4803] | —                 | 0.95  | 39.1320                     |
|                         |                  | 2        | [1.5210; 3.1630]       | [6.2093; 10.9868]   | [33.7845; 35.4990] | [1.3740; 3.2849]  | 0.95  | 37.5910                     |
| C <i>L. botrana</i>     | L2               | 1        | [2.0255; 2.6225]       | [6.1271; 9.6024]    | [34.2914; 34.9226] | —                 | 0.96  | 35.8079                     |
|                         |                  | 2        | [1.3984; 2.8880]       | [6.1536; 10.5254]   | [33.9871; 35.5662] | [1.2433; 2.4103]  | 0.96  | 34.7316                     |
| D <i>L. botrana</i>     | L3               | 1        | [2.1790; 2.6410]       | [6.7218; 9.4844]    | [33.9881; 34.0163] | —                 | 0.97  | 25.9150                     |
|                         |                  | 2        | [2.1555; 2.7908]       | [5.7067; 9.7287]    | [33.9916; 34.0112] | [1.7231; 2.4918]  | 0.97  | 25.2448                     |
| E <i>L. botrana</i>     | L4               | 1        | [2.0474; 2.6202]       | [7.3631; 10.6938]   | [33.9817; 34.0239] | —                 | 0.95  | 39.8082                     |
|                         |                  | 2        | [2.1800; 2.9619]       | [5.0696; 10.3314]   | [33.9964; 34.0044] | [1.8271; 3.0954]  | 0.95  | 31.9416                     |
| F <i>L. botrana</i>     | L5               | 1        | [1.1187; 1.3872]       | [6.1575; 9.3138]    | [33.9783; 34.0384] | —                 | 0.96  | 8.7283                      |
|                         |                  | 2        | [1.0971; 1.4630]       | [5.0716; 9.7113]    | [33.9814; 34.0306] | [1.6672; 2.5129]  | 0.96  | 8.6080                      |
| G <i>L. botrana</i>     | pupae            | 1        | [0.8726; 1.0373]       | [10.5052; 12.5814]  | [36.2264; 36.6180] | —                 | 0.98  | 3.5642                      |
|                         |                  | 2        | [1.0981; 1.2692]       | [8.9498; 11.0787]   | [36.0335; 36.1773] | [2.4499; 3.2304]  | 0.99  | 1.1190                      |
| H <i>M. sanguinipes</i> | nymphs           | 1        | [0.1450; 0.2350]       | [12.6611; 18.8346]  | [47.1770; 50.6419] | —                 | 0.86  | 2.0872                      |
|                         |                  | 2        | [0.1091; 0.5542]       | [1.8882; 22.5746]   | [43.8204; 49.2467] | [−3.2389; 11.665] | 0.86  | 1.9805                      |
| I <i>A. pisum</i>       |                  | 1        | [0.9560; 1.2855]       | [−2.0263; 1.98265]  | [31.2745; 33.3232] | —                 | 0.97  | 6.7491                      |
|                         |                  | 2        | [1.7974; 2.1779]       | [−10.7529; −1.4246] | [27.9777; 29.2406] | [3.1340; 7.5746]  | 0.98  | 4.0833                      |
| J <i>A. abdominalis</i> | egg              | 1        | [0.8127; 1.2583]       | [10.8399; 15.0175]  | [40.4419; 43.8506] | —                 | 0.96  | 8.7641                      |
|                         |                  | 2        | [1.4699; 2.5317]       | [8.5223; 14.0314]   | [37.4744; 40.2401] | [1.3354; 7.6650]  | 0.96  | 4.2624                      |
| K <i>H. zea</i>         | larvae and pupae | 1        | [0.1805; 0.2428]       | [10.0358; 12.4760]  | [40.2212; 43.8877] | —                 | 0.99  | 0.2260                      |
|                         |                  | 2        | [0.4067; 0.5639]       | [6.4880; 11.2886]   | [34.5714; 37.7764] | [1.8756; 10.328]  | 0.99  | 0.1745                      |
| L <i>H. zea</i>         | egg              | 1        | [1.9364; 2.5719]       | [9.5924; 12.3866]   | [38.6940; 41.1802] | —                 | 0.98  | 13.1198                     |
|                         |                  | 2        | [1.1366; 5.4542]       | [7.1999; 12.7714]   | [34.1753; 41.2244] | [0.6264; 5.2937]  | 0.98  | 12.0500                     |
| M <i>E. americana</i>   | egg              | 1        | [4.3373; 6.1804]       | [1.1666; 8.1065]    | [38.5178; 39.1159] | —                 | 0.94  | 845.1455                    |
|                         |                  | 2        | [3.5349; 6.4901]       | [1.1939; 9.5604]    | [38.3143; 39.5042] | [1.3193; 2.4118]  | 0.94  | 829.2774                    |

Table 4. Summary of developmental rate nonlinear model attributes.

| Model                        | Year | No. of Parameters | $T_0$ (°C) | $T_L$ (°C) |
|------------------------------|------|-------------------|------------|------------|
| Logan <i>et al.</i> (Eq. 6)  | 1976 | 4                 | —          | +          |
| Logan <i>et al.</i> (Eq. 10) | 1976 | 5                 | —          | +          |
| Hilbert and Logan (Eq. 6)    | 1983 | 5                 | +          | +          |
| Sharpe and DeMichelle        | 1977 | 6                 | —          | —          |
| Schoolfield <i>et al.</i>    | 1981 | 6                 | —          | —          |
| Lamb <i>et al.</i>           | 1984 | 4                 | —          | —          |
| Lactin <i>et al.</i>         | 1995 | 4                 | +          | —          |
| Briere <i>et al.</i> (Eq. 1) | 1998 | 3                 | +          | +          |
| Briere <i>et al.</i> (Eq. 2) | 1998 | 4                 | +          | +          |

Abbreviations:  $T_0$ : lower temperature threshold;  $T_L$ : upper temperature threshold. If a function incorporates a particular attribute or not, the value is + or —.

differences were between 0 and 1.14°C. Therefore, equations 1 and 2 allow precise estimation of the optimum temperature for a given data set.

When the lethal temperature estimated using equation 2 is lower than that estimated using equation 1, the parameter  $m$  was  $>2$ . Therefore, for  $m > 2$ , the developmental rate declines at temperatures above the optimum temperature more sharply and the maximum rate is more realistic; because the peak of the developmental rate is higher. However, there was a decrease in accuracy of the 2 thresholds at low and high temperatures by using equation 2 rather than equation 1. For  $m < 2$ , the curve is more symmetrical than for  $m = 2$  and will not necessarily give better results than using equation 1.

The models found in the literature whose features are presented in the Table 4 generally require from 4 to 6 parameters to estimate developmental rate, whereas equation 1 only requires 3. Hilbert and Logan (1983) reported that 5 descriptive parameters were sufficient for the description of the canonical form of the curve. We prove by our model and his results that 3 parameters are sufficient.

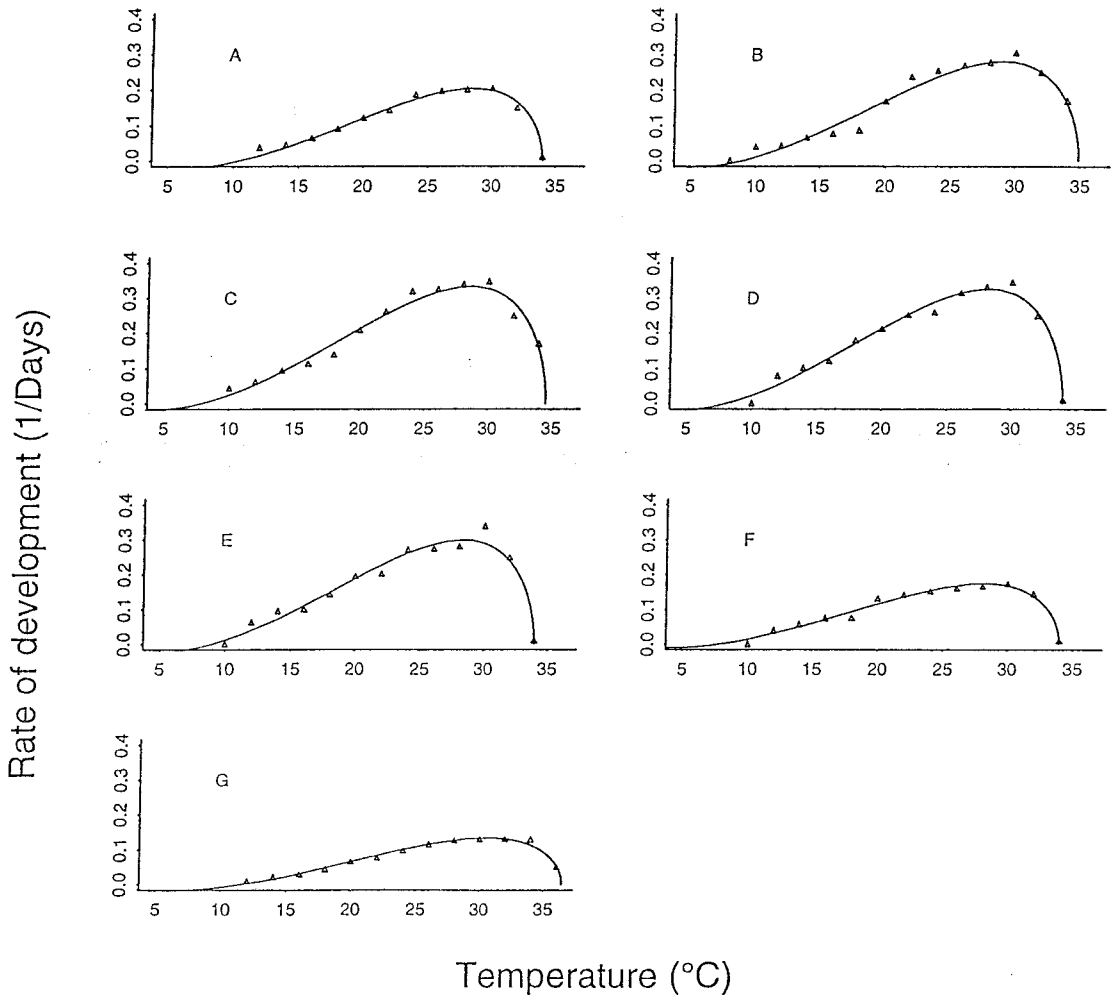


Fig. 1. Temperature-dependent developmental rates of *L. botrana*. (A) eggs. (B) First instars. (C) Second instars. (D) Third instars. (E) Fourth instars. (F) fifth instars. (G) Pupae. Solid line represents the fitted curve of equation 1.

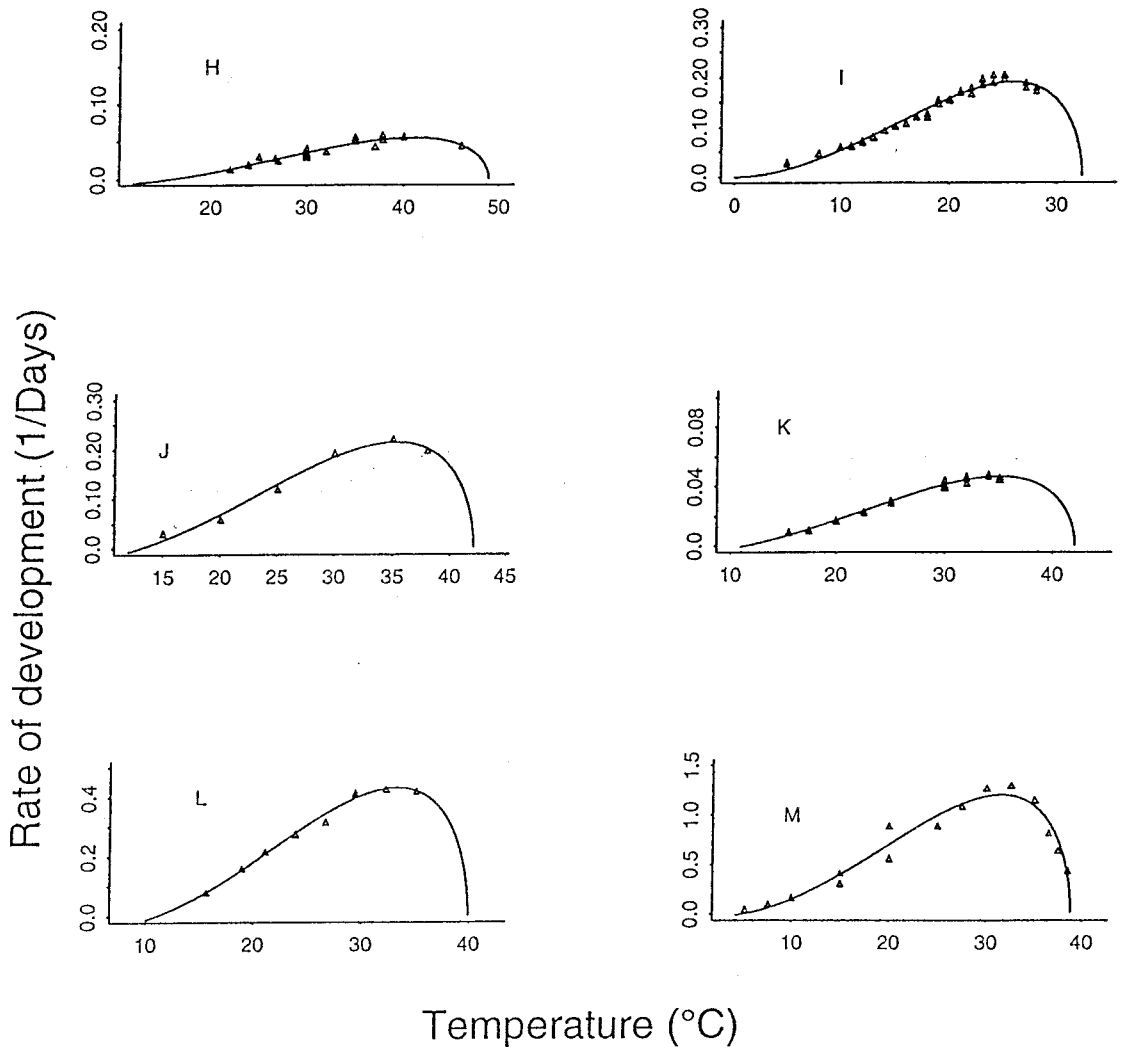


Fig. 2. Temperature-dependent developmental rates of 6 insect species. (H) *M. sanguinipes* nymphs. (I) *A. pisum*. (J) *A. abdominalis*. (K) *H. zea* larvae and pupae. (L) *H. zea* egg. (M) *E. americana* egg. Solid line represents the fitted curve of equation 1.

In addition, our 3 parameters also allow a descriptive interpretation like the parameters of Logan et al. (1976) and Lamb et al. (1984) and they are synonymous with the term "ecological parameters" used by Lamb et al. (1984). They do not have a biochemical meaning as in the Sharpe and DeMichele and the Schoolfield models, but rather a graphical interpretation.

It is useful for an equation to have parameters that can be interpreted graphically, which will allow initial parameter estimation fitting the curve by iterative nonlinear regression. The 2 parameters  $T_0$  and  $T_L$  determined by the intersection between the curve and the temperature axis have an obvious graphical interpretation. The 3rd parameter,  $a$ , also has a graphical interpretation and is a scaling parameter. The parameters of the Sharpe and DeMichele model have no simple graphical interpretation that provides initial

estimates from the usual inspection. All parameters of the Logan model (Logan 1988) or his improved version by Lactin et al. (1995) can also be interpreted graphically without any problem.

For equation 2, the  $m$  parameter can be considered a shape parameter, giving the spread of the curve, and is interpreted as the capacity of an insect species to develop and survive at high temperatures. If  $m < 2$ , then the capacity to survive at high temperatures is bigger. The curve of equation 2 will be more symmetrical around the optimum temperature and the decrease in developmental rate for temperatures above  $T_{opt}$  will be less sharp.

The thermal maximum or the thermal minimum values are not often included explicitly in the different models cited in the Table 3. Logan (1988) included in his model at least 1 of these parameters as Lactin et al.



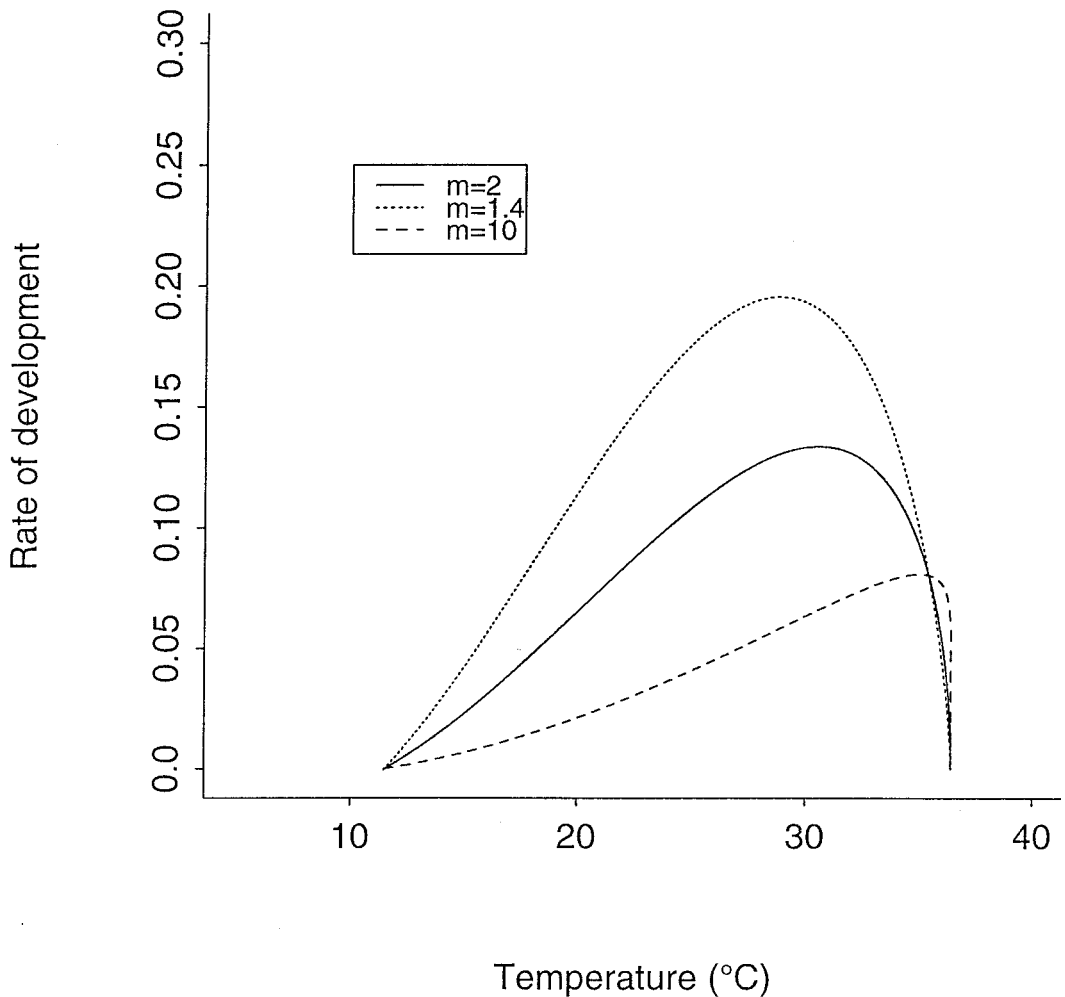


Fig. 3. Curves illustrating equation 2 for various values of  $m$ .

(1995) did; whereas, Sharpe and DeMichele (1977) and Schoolfield et al. (1981) did not use these 2 parameters. In some cases such as the Lamb et al. Model (1984), the optimum temperature has been preferred.

Our findings show that lower and upper thresholds are more important than the optimum temperature for an integrated pest management program and to evaluate the developmental rate of arthropods. However, it is more difficult to evaluate them experimentally. Indeed, insect development occurs within a defined temperature range. Near the point of zero, developmental insects often survive for long periods at cold temperatures with little or no development. For this reason, the temperature at which the development first occurs (i.e., the threshold) is difficult to measure accurately. At high temperatures, more and more individuals die making the study of developmental rate difficult. To estimate them accurately, data at low and high temperatures must be collected.

Equation 2 with a 4th parameter does not give a better description of the developmental rate than

equation 1, although the residual sums of squares are better because a greater divergence exists between observed and estimated thresholds at low temperatures.

Taking into consideration the simplicity of the new equation (1) and its adaptation to the criteria (estimation of upper and lower temperature thresholds, asymmetry about the optimum temperature, presence of an inflection point, and a sharp decline in development rate at high temperatures, the good values of estimated  $R^2$ ), it can be concluded from the results of this study that equation 1 has a wide range of application for insects. The nonlinear equation 1 can estimate developmental thresholds at low and high temperatures.

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