J. theor. Biol. (1981) **88,** 719–731

Non-linear Regression of Biological Temperature-dependent Rate Models Based on Absolute Reaction-rate Theory

R. M. SCHOOLFIELD, P. J. H. SHARPE AND C. E. MAGNUSON

Biosystems Research Division, Department of Industrial Engineering, Texas A&M University, College Station, Texas 77843, *U.S.A.*

(*Received* 27 *March* 1980, *and in revised form* 7 *September* 1980)

Biological temperature-dependent rate models based on Arrhenius' and Eyring's equations have been formulated by Johnson & Lewin (1946), Hultin (1955), and Sharpe & DeMichele (1977). The original formulation of Sharpe and DeMichele is poorly suited for non-linear regression. Very high correlations of parameter estimators occassionally make regression with their equation impossible using Marquardt's algorithm (1963).

This analysis describes a new formulation of Sharpe and DeMichele's model that greatly alleviates the non-linear regression problem. It is partly based on Hultin's formulation (1955). Biological and graphical interpretation of the model parameters is discussed. Regression suitability is illustrated with a typical data set. Similar modifications to the equations of Hultin (1955) and Johnson & Lewin (1946) are described.

1. Introduction

With the advent of computer simulation to the applied biological sciences, there has been an increased interest in the use of mathematical models to describe temperature-dependent rates of organism metabolism, growth and development. A review of the more popular models is given by Laudien (1973, pp. 359–361) and Watt (1968, pp. 276–281).

It is evident from these reviews that models based on Arrhenius' empirical equation (1) and Eyring's theoretical equation (2) have an advantage because of a foundation in absolute reaction-rate theory, as developed by Eyring (1935; Glasstone, Laidler & Eyring, 1941).

$$r(T) = A \,.\, \exp(-E_a/RT), \tag{1}$$

$$r(T) = \frac{\kappa KT}{h} \,.\, \exp[(\Delta S^{\neq} - \Delta H^{\neq}/T)/R] = B \,.\, T \,.\, \exp(-\Delta H^{\neq}/RT). \tag{2}$$

$r(T)$ is the rate constant of a (unimolecular) chemical reaction at temperature T (s^{-1}), A and B are pre-exponential factors (s^{-1}) or ($s^{-1}\,deg^{-1}$), E_a is the activation free energy (cal mol^{-1}), R is the universal gas constant

0022-5193/81/040719+13 $02.00/0

(1·987 cal mol^{-1} deg^{-1}), T is the temperature in K, $\Delta S^{\neq}$ is the entropy of activation (cal mol^{-1} deg^{-1}), $\Delta H^{\neq}$ is the enthalpy of activation (cal mol^{-1}), K is Boltzman's constant (cal $molecule^{-1}$ deg^{-1}), h is Planck's constant (cal s), κ is a transmission coefficient (unitless).

Johnson & Lewin (1946) and Hultin (1955) applied Eyring's theory to biological rate processes over high and low temperature regions, respectively. Sharpe & DeMichele (1977) combined these biological models into a unified rate model that described the rate of biological processes for all temperatures that support life.

Although these biological rate models have a theoretical advantage over their competitors, there has been one practical disadvantage to the use of these models. Fitting the models to observed development (or growth) rate data requires non-linear regression techniques. The original mathematical formulation of Sharpe and DeMichele's model is poorly suited for non-linear regression.

In this paper we describe a new formulation which greatly facilitates the model's use with non-linear regression techniques. We discuss the biological and graphical interpretations of the parameters in the new formulation and illustrate the regression suitability with a typical data set. We then describe similar modifications to the four parameter models of Hultin (1955), and Johnson & Lewin (1946). Although not discussed, similar modifications can be made to analogous models based on Arrhenius' equation (1) simply by eliminating the leading temperature factor.

2. Original Formulation

The model of Sharpe & DeMichele (1977) describes how the rate of a biological process is affected by temperature. In this discussion, we will consider the biological process to be the development of a poikilotherm (e.g. insect, plant, micro-organism, etc.), but metabolic processes such as growth, respiration or photosynthesis can also be described. The model is derived from the following assumptions: (1) at all temperatures, the development rate of a poikilotherm population is determined by a single rate-controlling enzyme reaction and (2) this rate-controlling enzyme is reversibly denatured (inactivated) at high and low temperatures, but maintains a constant total concentration (active + inactive) independent of temperature. The derivation of the original mathematical formulation from these assumptions is covered in detail by Sharpe & DeMichele (1977).

The original formulation is:

$$r(T) = \frac{T \cdot \exp\left[(\phi - \Delta H_A^{\neq}/T)/R\right]}{1 + \exp\left[(\Delta S_L - \Delta H_L/T)/R\right] + \exp\left[(\Delta S_H - \Delta H_H/T)/R\right]}. \quad (3)$$

$r(T)$ is the mean development rate at temperature T (time^{-1}), T is the temperature in K, R is the universal gas constant (1·987 cal deg^{-1} mol^{-1}). The other parameters in the equation are associated with the rate-controlling enzyme reaction.

ϕ is a conversion factor with no thermodynamic meaning†, $\Delta H_A^{\neq}$ is the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal mol^{-1}), ΔS_L is the change in entropy associated with low temperature inactivation of the enzyme (cal deg^{-1} mol^{-1}), ΔH_L is the change in enthalpy associated with low temperature inactivation of the enzyme (cal mol^{-1}), ΔS_H is the change in entropy associated with high temperature inactivation of the enzyme (cal deg^{-1} mol^{-1}), ΔH_H is the change in enthalpy associated with high temperature inactivation of the enzyme (cal mol^{-1}).

The difficulties of using this formulation with non-linear regression techniques are: (1) that very high correlations exist between model parameter estimators (e.g. 0·99996), and (2) that reasonable initial parameter estimates to begin iterations are not readily apparent.

With several data sets, very high correlations of parameter estimators have made regression impossible. These high correlations can be understood by looking at the partial derivatives of the model with respect to the different parameters. The partials with respect to ϕ and $\Delta H_A^{\neq}$; ΔS_L and ΔH_L; and ΔS_H and ΔH_H each differ by only the factor $-(1/T)$. This factor is almost constant since the Kelvin degree temperatures that support most life range only from 270–320 K. If this factor were constant, regression of the model would be impossible.

Initial parameter estimation for equation (3) is inconvenient because the parameters have no simple graphical interpretation that provides initial estimates from visual inspection. In the past, we have used fixed initial parameter estimates that are averages of previous least squares estimates.

3. Modified Formulation

The modified formulation is obtained by algebraic rearrangements of equation (3). There is no change in the theory of the model. In the modified form, three new thermodynamic parameters are defined to replace three parameters in equation (3).

The first new parameter, $\rho_{(25°C)}$, is defined as follows:

$$\rho_{(25°C)} = 298 \cdot e^{(\phi - \Delta H_A^{\neq}/298)/R}.$$

† By placing ϕ in the exponent, its units are physically inconsistent. This problem is corrected in the modified equation.

Solving for ϕ, we obtain

$$\phi = \frac{\Delta H_A^{\neq}}{298} + R \,.\, \ln \frac{\rho_{(25°C)}}{298},$$

and substituting into equation (3), the numerator becomes

$$\frac{T \,.\, \rho_{(25°C)}}{298} \exp\left[\frac{\Delta H_A^{\neq}}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right].$$

Thus $\rho_{(25°C)}$ replaces ϕ in the modified form.

The second new parameter, $T_{1/2_L}$, was defined by Hultin (1955).

$$T_{1/2_L} = \frac{\Delta H_L}{\Delta S_L}.$$

Solving for ΔS_L we obtain,

$$\Delta S_L = \frac{\Delta H_L}{T_{1/2_L}},$$

and substituting into equation (3), the second term of the denominator becomes

$$\exp\left(\frac{\Delta H_L}{R}\right)\left(\frac{1}{T_{1/2_L}} - \frac{1}{T}\right).$$

Thus $T_{1/2_L}$ replaces ΔS_L. The third parameter, $T_{1/2_H}$, is defined analogously to $T_{1/2_L}$.

Assembling the new numerator and denominator, the modified form of equation (3) becomes:

$$r(T) = \frac{\rho_{(25°C)} \dfrac{T}{298} \exp\left[\dfrac{\Delta H_A^{\neq}}{R}\left(\dfrac{1}{298} - \dfrac{1}{T}\right)\right]}{1 + \exp\left[\dfrac{\Delta H_L}{R}\left(\dfrac{1}{T_{1/2_L}} - \dfrac{1}{T}\right)\right] + \exp\left[\dfrac{\Delta H_H}{R}\left(\dfrac{1}{T_{1/2_H}} - \dfrac{1}{T}\right)\right]}. \quad (4)$$

$r(T)$ is the mean development rate at temperature $T(\text{time}^{-1})$, T is temperature in K (298 K = 25°C), R is the universal gas constant ($1{\cdot}987$ cal deg^{-1} mol^{-1}).

The other parameters in the equation are associated with the rate-controlling enzyme reaction.

$\rho_{(25°C)}$ is the development rate at 25°C assuming no enzyme inactivation (time^{-1}), $\Delta H_A^{\neq}$ is the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal mol^{-1}), $T_{1/2_L}$ is the temperature (°K) at which the enzyme is $\frac{1}{2}$ active and $\frac{1}{2}$ low temperature inactive, ΔH_L is the change in

enthalpy associated with low temperature inactivation of the enzyme (cal mol^{-1}), $T_{1/2_H}$ is the temperature (K) at which the enzyme is $\frac{1}{2}$ active and $\frac{1}{2}$ high temperature inactive, ΔH_H is the change in enthalpy associated with high temperature inactivation of the enzyme (cal mol^{-1}).

4. Interpretation of New Parameters

(A) BIOLOGICAL

One of the advantages of the new parameters is that they have more intuitive biological interpretations. To understand these biological interpretations, the significance of the denominator of equation (4) must be understood.

$$P_2(T) = \frac{1}{1+\exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2_L}}-\frac{1}{T}\right)\right]+\exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_{1/2_H}}-\frac{1}{T}\right)\right]}. \quad (5)$$

$P_2(T)$ represents the fraction of rate-controlling enzyme that is in the active state. As either the second or third term of the denominator in equation (5) increases in magnitude, the fraction of active rate-controlling enzyme decreases (due to either low temperature denaturation or high temperature denaturation, respectively). Sharpe & DeMichele (1977) have a complete discussion of the significance of equation (5), including graphs of $P_2(T)$.

The subscript of $\rho_{(25°C)}$ refers to 25°C (298 K) which was chosen as a standard reference temperature at which most poikilotherms experience little if any low or high temperature enzyme inactivation. Any temperature between 20°–30°C would fill this requirement for a reference temperature, but 25°C seemed the best choice, since it is used as a standard reference temperature in many scientific disciplines. Special cases of extremely thermophilic or psychrophilic organisms may indicate a different reference temperature.

The small enzyme inactivation at 25°C implies that, for most organisms, $P_2(298\text{ K}) \approx 1$. This implies that an approximate value for the rate of development at 25°C is the value of the numerator of equation (4) at 298 K. But at 298 K, the numerator is exactly equal to $\rho_{(25°C)}$. Thus $\rho_{(25°C)}$ is an approximate value for the rate of development at 25°C. Specifically, $\rho_{(25°C)}$ is an *exact* value for the rate of development at 25°C, *under the assumption* that there is no enzyme inactivation at 25°C [$P_2(298\text{ K}) = 1$].

The definition and interpretation of the second new parameter, $T_{1/2_L}$, was given by Hultin (1955). As the temperature decreases from 25°C, low

temperature enzyme inactivation will become significant (while high temperature inactivation remains negligible). At some temperature, T^*, half of the enzyme population becomes low temperature inactive and half remains active. Since $P_2(T^*) = \frac{1}{2}$, the second term of the denominator in equation (5) will be approximately equal to 1 (since the third term is negligible). This implies that $T^* = T_{1/2_L}$. Thus, the temperature at which the enzyme population is $\frac{1}{2}$ active and $\frac{1}{2}$ low temperature inactive is equal to $T_{1/2_L}$.† The interpretation of $T_{1/2}$ is analogous to that of $T_{1/2_L}$.

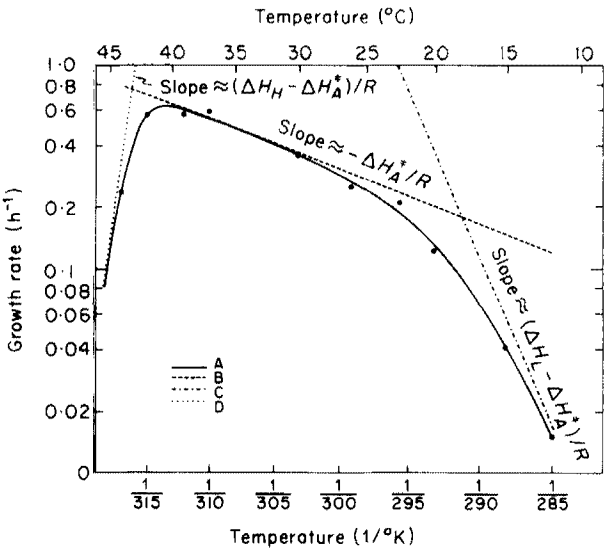

FIG. 1. Arrhenius plot (log rate vs. reciprocal degrees Kelvin) of specific growth rate (generations per hour) of *E. coli* in glucose-minimal medium (O'Donovan *et al.*, 1965) (·) = observed mean growth rates at 10 different temperatures. (A) = rates predicted by equation (4). (B) = plot of equation (4) numerator. (C) and (D) = plots of equation (4) numerator divided by second and third term of denominator, respectively. The slopes of lines (B), (C) and (D) are related to enthalpy parameters, as described in the text.

(B) GRAPHICAL

All six parameters of equation (4) have graphical interpretations when viewed on an Arrhenius plot (log of development rate vs. reciprocal Kelvin temperature). Figure 1 shows an example of poikilotherm growth rate data, describing the specific growth rate (generations per hour) of *Escherichia coli* in glucose-minimal medium (O'Donovan, Kearney & Ingraham, 1965). The

† An equivalent definition for $T_{1/2_L}$ is the temperature at which the standard Gibbs free-energy change ($\Delta G°$) for the low temperature inactivation reaction is equal to zero (assuming negligible high temperature inactivation).

J. theor. Biol. (1981) **88,** 733–742

Non-linear Benefits and the Evolution of Eusociality in the Hymenoptera

ROBERT ABUGOV

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, *U.S.A.*

(*Received* 1 *August* 1980, *and in revised form* 17 *September* 1980)

A general model for examining the evolution of social behavior is developed which does not require that benefits received be linear functions of the number of social donors encountered. The subsocial route for the evolution of eusociality in haplodiploid organisms is then examined within the context of this model Non-linearities render conditions for frequency independent fixation or loss of sister helping alleles more stringent than expected from models based on the assumption of linear benefits. In particular, both stable polymorphisms and frequency dependent selective thresholds for sister helping behaviour may commonly obtain.

Consider the following evolutionary scenario. A long-lived Hymenopteran mother continues to lay eggs at the same nest from which her earlier offspring have been hatched. A mutation causes one of her female offspring to forego raising daughters in favor of raising sisters who will later reproduce. Fixation of this new allele which codes for altruistic behavior on alternate generations results in the formation of a eusocial species.

That this scenario has held for most eusocial Hymenoptera is the prevalent view among most students of insect sociality (e.g. recent reviews by Evans & West Eberhard, 1970; Wilson, 1975; Starr, 1979), although it seems plausible that this "subsocial" route to eusociality was not taken by most non-allodapine bees (Michener, 1974). The purpose of the present study is to examine the evolutionary dynamics of the allele for sister-raising.

A rather fragile assumption upon which previous studies addressing this topic (West Eberhard, 1975, after Hamilton, 1964; Craig, 1979) depend is relaxed in this study. In particular, this treatment will not require that the benefit accrued to a recipient be a linear function of the number of social donors with which she interacts. Relaxation of this requirement permits the inclusion of social interactions which are biologically more realistic. As an example, consider food donations by altruists. In a bad year, a recipient catered to by only one altruist may gain only a negligible increment in fitness, while a recipient with two altruists may gain more than double that increment. This makes the increment gained as a function of the number of

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The three new parameters determine the intercepts of lines (B), (C), and (D) in Fig. 1. This is shown in Fig. 2. Since line (B) in Fig. 2 [same as line (B) in Fig. 1] represents the rate if no enzyme inactivation occurred, this line must pass through the x, y co-ordinates $[1/298, \rho_{(25°C)}]$. Thus, $\rho_{(25°C)}$ determines the intercept of line (B) at $T = 298$ K.

Line (C) in Fig. 2 shows rates equal to half of line (B). These lines are parallel since the rates are on a log scale. Line (C) represents the rate if only half the enzyme population were active at all temperatures $[P_2(T) = \frac{1}{2}]$. The temperatures (high and low) where curve (A) passes through line (C) are $T_{1/2_H}$ and $T_{1/2_L}$, respectively. Thus, $T_{1/2_H}$ and $T_{1/2_L}$ determine, albeit indirectly, the intercepts of lines (C) and (D) in fig. 1.

5. Regression Suitability

The same very high correlation between parameter estimators is not expected when the partials of the model with respect to the new parameters are considered. In the three cases, $\Delta H_A^{\neq}$ and $\rho_{(25°C)}$, ΔH_L and $T_{1/2_L}$, and ΔH_H and $T_{1/2_H}$, the ratio of the model partial derivatives are

$$\left(\frac{1}{298} - \frac{1}{T}\right) \cdot \frac{\rho_{(25°C)}}{R},$$

$$\left(\frac{1}{T} - \frac{1}{T_{1/2_L}}\right) \cdot \frac{T_{1/2_L}^2}{\Delta H_L},$$

and

$$\left(\frac{1}{T} - \frac{1}{T_{1/2_H}}\right) \cdot \frac{T_{1/2_H}^2}{\Delta H_H}$$

respectively. Each of these ratios has a wide magnitude range, because the first factor of each ratio changes sign as T varies from 260 to 340 K. Thus we would not expect very high correlations in general.

The alleviation of the correlation problem as well as the initial parameter estimate selection problem can be illustrated with the example of the *E. coli* data in Fig. 2. Using Marquardt's search algorithm, (Marquardt, 1963; Bevington, 1969), we performed a least squares non-linear regression on these data (weighted according to the reciprocal of the rate values, since low rates tend to be measured with greater accuracy than high rates).

The simple graphical interpretations of $\rho_{(25°C)}$, $T_{1/2_L}$, and $T_{1/2_H}$ in equation (4) allowed us to obtain starting estimates for these parameters within one order of magnitude of the least squares estimates. From Fig. 2, we can estimate $\hat{\rho}_{(25°C)} \simeq 0{\cdot}3\ \mathrm{h}^{-1}$, $\hat{T}_{1/2_L} \simeq 290$ K, and $\hat{T}_{1/2_H} \simeq 315$ K. Because

starting estimates for $\Delta H_A^{\neq}$, ΔH_L and ΔH_H are not as readily apparent by graphical inspection, fixed starting estimates (averages of previous estimates) of $\Delta H_H = 10\,000$ cal mol^{-1}, $\Delta H_L = -60\,000$ cal mol^{-1}, and $\Delta H_H = 100\,000$ cal mol^{-1} were used. In equation (3), however, all starting parameter estimates must be fixed, since ϕ, ΔS_L, and ΔS_H have no simple graphical interpretation. These were $\hat{\phi} = 20$, $\Delta S_L = -200$ cal deg^{-1} mol^{-1}, and $\Delta S_H = 300$ cal deg^{-1} mol^{-1}.

TABLE 1

Least squares parameter estimates for specific growth rate of E. coli *in glucose-minimal medium* (*O'Donovan* et al., 1965) (*Fig.* 1)

Using equation (3)	ϕ †	$\Delta H_A^{\neq}$ cal/mol	ΔS_L cal/mol −°K	ΔH_L cal/mol	ΔS_H cal/mol −°K	ΔH_H cal/mol	s_e^2	Number of iterations for convergence
Estimate	19·51	9963	−176·9	−51510	676·2	214 000	$9{\cdot}09\times10^{-4}$	14
Using equation (4)	$\rho_{(25°C)}$ h^{-1}	$\Delta H_A^{\neq}$ cal/mol	$T_{1/2L}$ °K	ΔH_L cal/mol	$T_{1/2H}$ °K	ΔH_H cal/mol	s_e^2	Number of iterations for convergence
Estimate	0·273	9963	291·2	−51510	316·4	214 000	$9{\cdot}09\times10^{-4}$	7

† By placing ϕ in the exponent, its units are physically inconsistent. This problem is corrected in the modified equation.

Table 1 shows the least squares estimates of the parameters and the residual mean square (s_e^2) for equations (3) and (4). Both equations predict the same estimated rates with the same residual mean square.

Equation (4), however, required half as many iterations for convergence as equation (3). With a convergence criterion of

$$\frac{RSS_n - RSS_{n+1}}{RSS_{n+1}} < 10^{-8},$$

where RSS_n = the weighted residual sum of squares after the nth iteration, equation (4) required seven iterations for convergence while equation (3) required 14 (Table 1).

The primary reason for the slow convergence of equation (3) is the very high correlations of certain parameter estimators (Table 2). Note that the correlations between ϕ and $\Delta H_A^{\neq}$, ΔS_L and ΔH_L, and ΔS_H and ΔH_H are all greater than 0·9998.

TABLE 2

Asymptotic correlation matrix of equation (3) *parameter estimators for specific growth rate of* E. coli *in glucose-minimal medium* (*O'Donovan* et al., 1965) (*Fig.* 1)

	ϕ	$\Delta H_A^{\neq}$	ΔS_L	ΔH_L	ΔS_H	ΔH_H
ϕ	1	0·99993	−0·74	−0·73	−0·50	−0·50
$\Delta H_A^{\neq}$	0·99993	1	−0·74	−0·73	−0·49	−0·49
ΔS_L	−0·74	−0·74	1	0·9998	0·24	0·24
ΔH_L	−0·73	−0·73	0·9998	1	0·24	0·24
ΔS_H	−0·50	−0·49	0·24	0·24	1	0·999996
ΔH_H	−0·50	−0·49	0·24	0·24	0·999996	1

Table 3 shows that this difficulty has been alleviated with equation (4). Note that the highest correlation for equation (4) is 0·96 (in absolute value). We feel that this example is representative of the type of regression benefits that equation (4) generally provides when compared to equation (3).

TABLE 3

Asymptotic correlation matrix of equation (4) *parameter estimators for specific growth rate of* E. coli *in glucose-minimal medium* (*O'Donovan* et al., 1965) (*Fig.* 1)

	$\rho_{(25°C)}$	$\Delta H_A^{\neq}$	$T_{1/2L}$	ΔH_L	$T_{1/2H}$	ΔH_H
$\rho_{(25°C)}$	1	−0·96	0·95	0·79	0·58	0·36
$\Delta H_A^{\neq}$	−0·96	1	−0·93	−0·73	−0·74	−0·49
$T_{1/2L}$	0·95	−0·93	1	0·79	0·59	0·37
ΔH_L	0·79	−0·73	0·79	1	0·40	0·24
$T_{1/2L}$	0·58	−0·74	0·59	0·40	1	0·73
ΔH_H	0·36	−0·49	0·37	0·24	0·73	1

6. Four Parameter Models

In order to estimate the enzyme inactivation parameters ($T_{1/2_L}$, ΔH_L, $T_{1/2_H}$, ΔH_H), development rate data must be obtained in both regions of Arrhenius non-linearity. This may be a formidable experimental task. Often, however, there are situations where the temperature response of a poikilotherm has been studied for only part of the temperature spectrum. For example, in insect emergence from diapause, a researcher may have much more data and interest in the insect development rate at cold temperatures than at very warm temperatures.

In such a situation, equation (4) can be modified to eliminate the high temperature enzyme inactivation effect. This is done by removing the last exponential term in the denominator to give a four parameter model:

$$r(T) = \frac{\rho_{(25°C)} \dfrac{T}{298} \exp\left[\dfrac{\Delta H_A^{\neq}}{R}\left(\dfrac{1}{298} - \dfrac{1}{T}\right)\right]}{1 + \exp\left[\dfrac{\Delta H_L}{R}\left(\dfrac{1}{T_{1/2_L}} - \dfrac{1}{T}\right)\right]}. \tag{6}$$

Equation (6) is analogous to Hultin's equation (1955) and can be used in situations where high temperature inactivation has not been studied (i.e. the temperature optimum for development or growth has not been found). Figure 3 shows this four parameter model fitted to prepupal development rate data (h^{-1}) for *Drosophila melanogaster* below 28°C (Bliss, 1926).

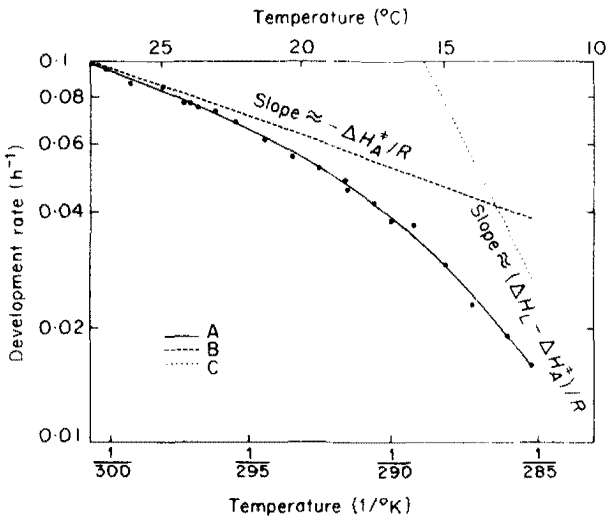

FIG. 3. Arrhenius plot of prepupal development rate (hr^{-1}) for *Drosophila melanogaster* below 28°C (Bliss, 1926) (·) = observed mean development rates at 20 different temperatures. (A) = rates predicted by equation (6). (B) = plot of equation (6) numerator. (C) = plot of equation (6) numerator divided by exponential term of denominator.

Low temperature inactivation can also be removed giving a four parameter model with only high temperature inactivation:

$$r(T) = \frac{\rho_{(25°C)} \dfrac{T}{298} \exp\left[\dfrac{\Delta H_A^{\neq}}{R}\left(\dfrac{1}{298} - \dfrac{1}{T}\right)\right.}{1 + \exp\left[\dfrac{\Delta H_H}{R}\left(\dfrac{1}{T_{1/2_H}} - \dfrac{1}{T}\right)\right]}. \tag{7}$$

This equation is analogous to the equation developed by Johnson & Lewin (1946). Figure 4 shows this four-parameter model fitted to immature development rate data ($days^{-1}$) for the boll weevil (*Anthonomus grandis*) (Sharpe *et al.*, 1977).

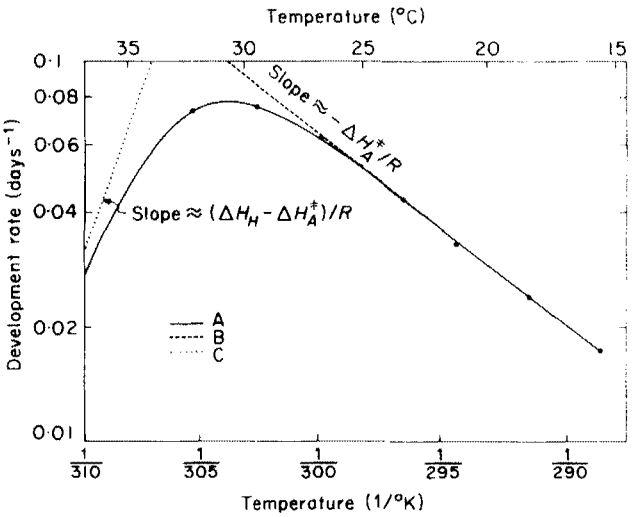

FIG. 4. Arrhenius plot of immature development rate ($days^{-1}$) for the boll weevil (*Anthonomus grandis*) (Sharpe *et al.*, 1977) (·) = observed mean development rates at seven different temperatures. (A) = rates predicted by equation (7). (B) = plot of equation (7) numerator. (C) = plot of equation (7) numerator divided by exponential term of denominator.

7. Conclusion

The modification of these biological temperature-dependent rate models to employ $\rho_{(25°C)}$, $T_{1/2_D}$ and $T_{1/2_H}$ provides three advantages: (1) better biological and graphical parameter interpretations, (2) more convenient initial parameter estimates, and (3) reduced correlation between parameter estimators. Use of equations (4), (6) and (7) should alleviate the non-linear regression problem associated with the application of biological temperature-dependent rate models based on either absolute reaction-rate theory or Arrhenius' empirical equation.

This study was supported in part by the National Science Foundation (grant NEB 77-14406), in part by a United States Department of Agriculture sponsored program entitled "The Expanded Southern Pine Beetle Research and Applications Program" [grant 89-106 (19-317)], and in part by a United States Department of Agriculture SEA co-operative agreement (58-9AHZ-9-365). The findings, opinions, and recommendations expressed herein are those of the authors and not necessarily those of the NSF or the USDA.

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