

An Analytic Model for Description of Temperature Dependent Rate Phenomena in Arthropods¹

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ABSTRACT

A new description of temperature-dependent, rate phenomena was deduced to describe developmental time and ovipositional data for the McDaniel spider mite, *Tetranychus mcdanieli* McGregor. The derived equation accounted for asymmetry about optimum temperature and was of particular utility for description of systems operating at or above optimum temperatures. Ovipositional and developmental rate functions were used in a temperature-driven, discrete-time, simulation model describing McDaniel spider mite population dynamics. Temperature dependence of the instantaneous population growth rate was determined by fitting the derived rate-temperature function to data generated through simulation at various fixed temperatures. The functional relationship of important population parameters to temperature provided the mechanism for inclusion of phenological effects on mite populations in a synoptic apple pest management model.

Two derived functions were fit to several published rate-temperature data sets. Adequacy of description (as indicated by R^2 values) indicated general applicability of both functions for description of temperature-controlled, biological processes. Further, it was concluded that the singular perturbation method of matched asymptotes has potentially wide application in ecology, and an Appendix detailing the application of this method is included.

The McDaniel spider mite, *Tetranychus mcdanieli* McGregor, has been recognized as a significant pest on apples in Washington state since 1951, and has probably been a problem since apples were first produced in the interior valleys of the state. The critical importance of temperature to development of mite populations has long been recognized, and a good deal of experimental effort has been expended determining temperature dependence of life history parameters for this species (Tanigoshi et al. 1975). We felt methods available for analytic description of temperature-dependent, life history parameters were inadequate. The day-degree concept with its inherent linearity is particularly invalid for mite populations. Tanigoshi et al. (1975) used least squares polynomials to describe temperature dependent life history parameters in *T. mcdanieli*, but behavior of these curves was questionable at temperatures near or above optimum. An inadequate description was particularly noticeable for temperatures above optimum but within a range common under field conditions during July and August. Application of empirical methods for describing high temperature response was further complicated by the difficulty in obtaining reliable experimental data at these temperatures when the system was undergoing rapid change. Other empirical functions (Parker 1974, Messenger and Flitters 1958), with well defined behavior throughout an interval, have been successfully used

to describe temperature-dependent, metabolic processes. However, for many simulation purposes, a function described by biologically meaningful (measurable) parameters is superior to a purely empirical form. This is particularly true for initial stages of mathematical modeling when the actual data base may be weak. In these circumstances response functions must be based primarily on an experienced researcher's intuition and it may, in fact, be impossible to use a purely empirical form. Deductive equations (at least in part) have been proposed by Pradhan (1946) and Stinner et al. (1974). Both equations are unsatisfactory due to symmetry about optimum temperature, a situation which is obviously not true for the considered mite population (Tanigoshi et al. 1975). Therefore, a method for analytic expression of temperature-dependent, physiological phenomena was considered in some detail.

Development of Temperature Curve

The effect of temperature on life history parameters, initially developmental time, is broken into 2 phases (Fig. 1). Phase I, characterized by a monotone increasing slope, is used to describe behavior from some base to optimum temperature. Phase II occurs once optimum temperature has been exceeded and is characterized by a precipitous decline in rate until the lethal, maximum temperature is reached. When viewed in this manner, the problem is analogous to certain "boundary layer" problems in the physical sciences, and the method of matched asymptotic expansions is used to obtain a solution (Lin and Segel 1974, Appendix). Briefly, the technique is to find separate but related solutions describing the behavior during Phase I and Phase II. From these 2

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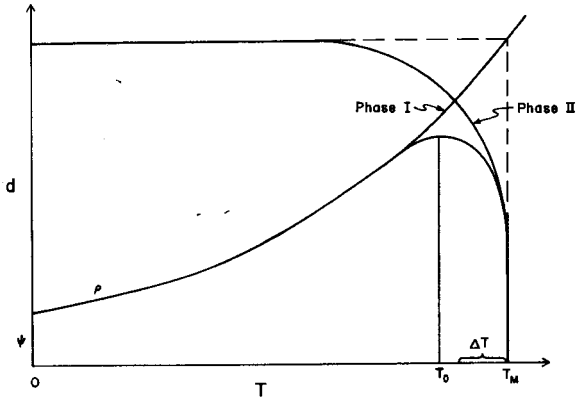


FIG. 1.—Model for developmental rate as a function of temperature.

solutions, if certain conditions are met, a single analytic solution is obtained describing the entire range of behavior.

Following an argument advanced by Pradhan (1946) relating rate of development to the rate of enzyme-catalyzed, biochemical reactions, an outer (low temperature) solution can be derived of the form,

$$d_o(T) = \psi \exp(\rho T) \quad (1)$$

where ψ is developmental rate at some base temperature above developmental threshold; ρ is the rate increase to optimum temperature; and T is degrees above base temperature (T_b).

The exact nature of physiological processes which lead to mortality at high temperatures are not well understood. Mortality may be due to heat denaturation of one or more critical enzymes, or to dissociation of the epicuticle, monomolecular wax layer, and subsequent desiccation (Beament 1958). Therefore, the solution during Phase II is motivated by the empirical response during high temperature decline. To facilitate description in this interval the scaled variable τ is introduced (see Appendix for motivation behind choice of τ)

$$\tau = (T_M - T) / \Delta T, \quad (2)$$

where T_M is the lethal, maximum temperature in

degrees above T_b ; and ΔT is the width of the high temperature boundary layer. The function

$$d_i(\tau) = C_o [1 - \exp(-\tau)] \quad (3)$$

is used to describe behavior during Phase II. This resulted in 2 scales, τ inside the high temperature boundary layer and T outside. At this point we have,

$$d(T) \sim \begin{cases} d_o(T) = \psi \exp(\rho T) & \text{for } T \text{ in Phase I} \\ d_i(\tau) = C_o [1 - \exp(-\tau)] & \text{for } T \text{ in Phase II} \end{cases} \quad (4)$$

which leaves 2 unresolved matters: namely, what value should be chosen for the constant C_o , and how can we develop an expression uniformly valid over the entire interval $[T_b, T_M]$ from these outer and inner solutions? The answer to the 1st question is provided by the intermediate limit technique of matching which resulted in the condition (see Appendix)

$$d_o(T_M) = \lim_{\tau \rightarrow \infty} d_i(\tau) = C_o = \psi \exp(\rho T_M). \quad (5)$$

Then a uniformly-valid, asymptotic expansion over the interval $[T_b, T_M]$ was obtained by substituting the result of (5) into (3), adding the 2 solutions of (4) together, and subtracting their common limit as determined by (5). This uniformly valid additive composite is given by

$$d(T) = \psi [\exp(\rho T) - \exp(\rho T_M - \tau)]. \quad (6)$$

Equation (6) has several desirable characteristics. It is analytic over the entire range of temperatures and is described by parameters which are measurable with biological (or at least partially biological) interpretation. ψ is a directly measurable rate of the temperature-dependent, physiological process at some base temperature; ρ can be interpreted as a composite Q_{10} value for critical enzyme-catalyzed, biochemical reactions; T_M is a thermal maximum (temperature at which life processes can no longer be maintained for prolonged periods of time); and ΔT is the temperature range over which 'thermal breakdown' becomes the overriding influence.

In addition to analytic and biological acceptability, the function provided a good description of rate-temperature data, as shown by the least squares fit to developmental rate for protonymph (Fig. 2a). To account for nonlinearity in the transformation from

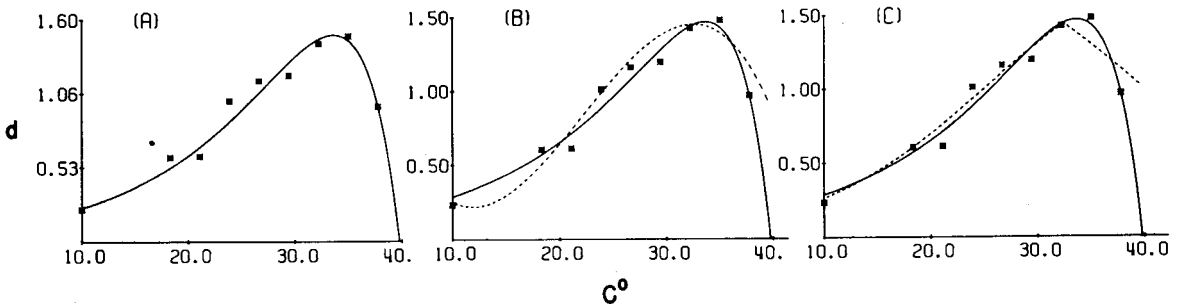


FIG. 2.—a. Least squares fit of equation (6) to developmental rate for *T. mcdanieli* protonymph (data from Tanigoshi et al. 1975a); b. Comparison of least squares polynomial to equation (6); c. Comparison of the modified sigmoid function to equation (6).

Table 1.—Residual sums of squares for least squares fit for 3rd degree polynomial, modified sigmoid function and equation (6).

Life stage	Residual sums of squares		
	Polynomial	Modified sigmoid ^b	Equation (6)
Larvae ^a	.1016	.2351	.0470
Protonymph ^a	.0845	.0997	.0519
Deutonymph ^a	.0415	.0976	.0370

^a Data from Tanigoshi et al. 1975.

^b Stinner et al. 1974.

developmental period to rate of development, data points in Fig. 2a were computed as

$$\bar{d} = 1 / \exp\left[\frac{\sum_{i=1}^n \ln(D_i)}{n} \right],$$

where \bar{d} is average rate of development; D_i 's are observed developmental times; and n is sample size. Non-linear least squares fits were made for active, immature life stages using Harwell Library Subroutine VAO5A (Powell 1968). Initial estimates of T_M and ΔT were visually made from the data; ψ was initialized to the observed developmental rate at the base temperature; and ρ was initially estimated by solving (1) using ψ and the observed maximum d_o (note that the independent variable is measured in degrees above T_b).

A comparison was made of the derived equation to a 3rd degree polynomial (degree determined by F test at 5% significance level) and a modified sigmoid function (Stinner et al. 1974). Since all 3 functions are defined by 4 parameters, a valid measure of goodness of fit is obtained by comparing magnitudes of the respective Residual Sums of Squares. As shown in Table 1, an improved fit was obtained in all cases by use of equation (6). Comparison to the fitted polynomial is shown in Fig. 2b. Both functions provide an adequate fit for mid-range temperatures, but the polynomial exhibits erratic behavior at both extremes. A similar comparison to the modified sigmoid function is shown in Fig. 2c. Both functions describe the data quite well at low and intermediate temperatures, however, the artificially imposed symmetry of the modified sigmoid function about opti-

mum temperature results in an inadequate description above thermal optimum. Additionally, equation (6) is analytic for all temperatures in the interval $[T_b, T_M]$.

The mathematical technique of matched asymptotic expansions used to derive (6) has wide ecological application. Conceptual formulation is often facilitated by decomposition of complex ecological phenomena into 2 (or more) distinct phases. Matched asymptotes, in effect, provide an analytic solution which is bounded by the separate curves describing individual phases. For example, in an attempt to demonstrate general application, equation (6) was fit to several published data sets. When these functions, were plotted it became apparent that response in the low-to-mid-temperature range (Phase I) was more sigmoid than could be accounted for by (6). Motivated by this sigmoid behavior (see Appendix), an outer expansion satisfying

$$\dot{d}_o(T) = d(\rho - \gamma d); d_o(0) = \psi \quad (7)$$

was used for Phase I description. Solving (7) resulted in

$$d_o(T) = \alpha[1 + k \exp(-\rho T)]^{-1} \quad (8)$$

for $\alpha = \rho/\gamma$, and $k = (\alpha - \psi)/\psi$.

Using the inner expansion given by (3), with the matching condition

$$d_o(T_M) = \lim_{\tau \rightarrow \infty} d_i(\tau) \Rightarrow C_o = d_o(T_M) \cong \alpha, \quad (9)$$

we obtain the uniformly-valid, additive composite given by

$$d = \alpha\{[1 + k \exp(-\rho T)]^{-1} - \exp(-\tau)\}. \quad (10)$$

Equations (6) and (10) were fit to diverse, published data sets, including developmental rate for several insect species, oviposition for the McDaniel spider mite, and rate of sucrose oxidation for 2 bacterial species. Results of these least square fits are listed in Table 2, and three typical, comparative plots are shown in Fig.3. The extremely good fit, particularly when using equation (10), indicates broad application for description of temperature-related, biological processes.

It should be noted that equation (7) is not entirely

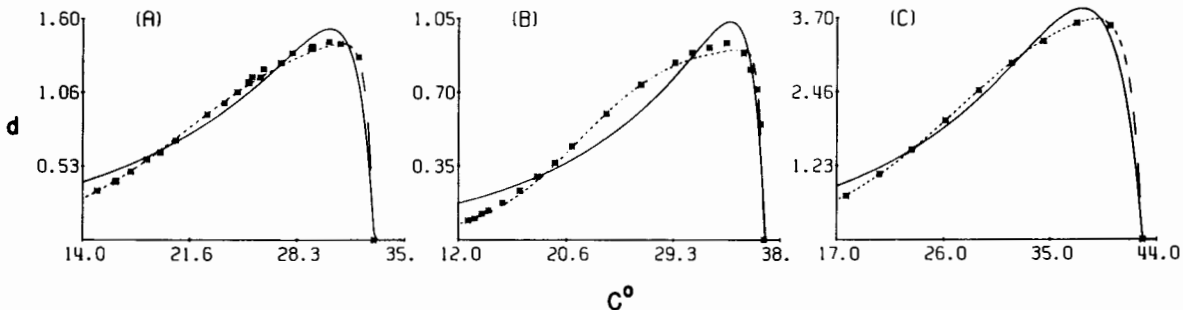


FIG. 3.—Comparative plot of exponential outer expansion (solid line) to sigmoid outer expansion (broken line) for: a. Rate of egg development for *Drosophila melanogaster*. b. Rate of egg development for *Dacus dorsalis*. c. Rate of egg development for *Lucilia sericata*. Dimension of dependent variable is proportion development completed per day.

Table 2.—Comparative R^2 values for equation (6) with exponential outer expansion [$(R^2)_1$] and for equation (10) with sigmoid outer expansion [$(R^2)_2$].

Data source	No. of data points	$(R^2)_1$	$(R^2)_2$
<i>Dacus dorsalis</i> Hendel, rate of egg development ^a	20	.9279	.9930
<i>Drosophila melanogaster</i> Meigen, rate of egg development ^b	23	.9649	.9967
<i>D. melanogaster</i> , rate of pupal development ^c	16	.9332	.9453
<i>Phormia regina</i> (Meigen), rate of egg development ^d	11	.9795	.9957
<i>Cochliomyia macellaria</i> (Fab.), rate of egg development ^d	10	.9858	.9999
<i>Lucilia</i> (= <i>Phaenicia</i>) <i>sericata</i> (Meigen), rate of egg development ^d	10	.9965	.9993
<i>Musca domestica</i> L., rate of egg development ^d	11	.9864	.9997
<i>Ephestia</i> (= <i>Anagasta</i>) <i>kuehniella</i> (Zeller), rate of egg development ^e	14	.9741	.9873
<i>Bacillus psychrophilus</i> , rate of sucrose oxidation ^f	6	.9984	.9999
<i>Bacillus thuringiensis</i> , rate of sucrose oxidation ^f	9	.9134	.9759
<i>T. mcdanieli</i> , total oviposition ^g	7	.9243	.9401

^a Messenger and Flitters, 1958.
^b Powsner, 1935.
^c Ludwig and Cable, 1933.
^d Melvin, 1934.

^e Voute, 1936.
^f Stokes and Larkin, 1968.
^g Tanigoshi, et al., 1975.

without biological interpretation since ρ can be interpreted exactly as in (1) and γ may be considered a temperature denaturization effect. Equation (10) can be viewed as an extension of (6) to allow high temperature decline due to both desiccation and enzyme denaturization. Parameter initialization for non-linear least squares estimates given in Table 2 were made by setting

$$\begin{aligned} \rho_2 &= 2 \rho_1 & a. \\ \gamma &= \rho_2 / d_M \text{ for } d_M = \text{maximum} & b. \\ & \text{observed} \\ & \text{rate} \end{aligned}$$

$$\begin{aligned} (T_M)_2 &= (T_M)_1 & c. \\ (\Delta T)_2 &= .5(\Delta T)_1 & d. \\ k &= (\rho_2 / \gamma - \psi_2) / \psi_2 \text{ where } \psi_2 = \psi_1 & e. \end{aligned} \tag{11}$$

where the subscripts 1 and 2 refer to equations (6) and (10) respectively. A detailed description of the mathematical motivation behind application of matched asymptotes to our temperature problem is given in the Appendix.

Application to Population Simulation

Since equation (6) describes the rate of development, the proportion of the i -th life stage completed during a time interval $[t_1, t_2]$ is given by

$$\int_{t_1}^{t_2} d_i[T(t)]dt \tag{12}$$

where d_i is obtained from equation (6) or (10) with parameters describing developmental rate for the i th life stage, and temperature (T) is a function of time (t). By assuming (a) the effect of temperature on development is additive (Tanigoshi et al. 1976), and (b) a constant temperature during some small interval of time (Δt) equation (12) is approximated by

$$\sum_{j=1}^n d_i(T_j)\Delta t \text{ for } n \Delta t = t_2 - t_1. \tag{13}$$

An example of protonymph developmental rate over

a 12-h temperature profile ($\Delta t = 1$ hr.) is shown in Fig. 4. To determine the effect of temperature on the population dynamics of *T. mcdanieli*, it was necessary to incorporate the temperature-rate equation into a synoptic model describing a complete life history. This was accomplished by formulating a discrete time simulation model using equation (6) to update each life stage and computing oviposition from the curve shown in Fig. 5. The maximum population growth rate possible at a given temperature

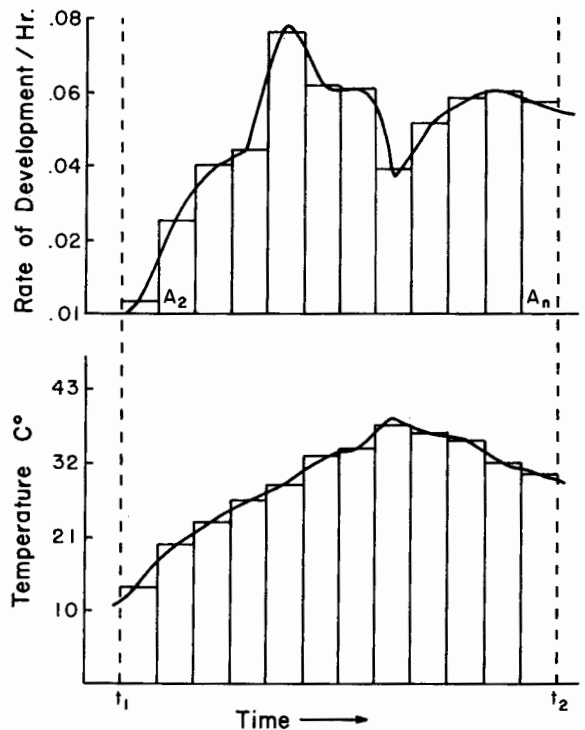


FIG. 4.—Twelve hour temperature profile and corresponding rate of development for *T. mcdanieli* protonymph. Life stage is completed when the sum of the areas (A_1) equals 1.

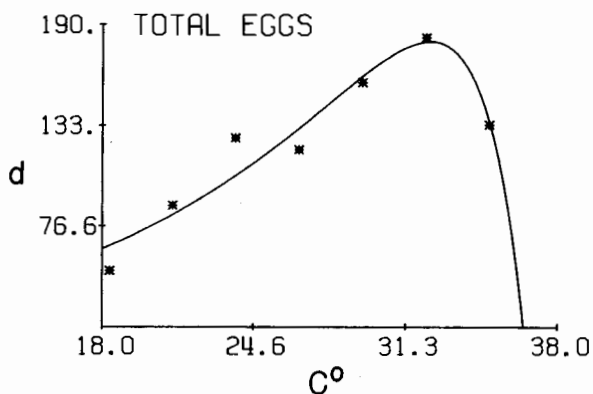


FIG. 5.—Equation (6) fit to total oviposition for *T. mcdanieli*.

$r_m(T)$ was estimated from the discrete time model by computing the population growth rate $r(T)$ at each time step and allowing enough time for convergence of $r(T)$ to $r_m(T)$. A least squares fit of (6) to these generated data points resulted in (see Fig. 6)

$$r_m = .048 [\exp(.103 T) - \exp\{2.89 - (28.04 - T)/2.71\}]. \quad (14)$$

Solving for the 1st derivative of (14) set to zero (see Appendix) resulted in an estimated optimum temperature of 33.24 ($r_m(T = T_o) = .38$).

Through the same reasoning that led to equations (12) and (13), equation (14) can be used to predict population response over any given temperature regime. The derived equation provides a valuable pest management tool for predicting the likelihood of mite population outbreaks, and more importantly provides a sound basis for inclusion of phenological effects on mite populations in a synoptic apple production model.

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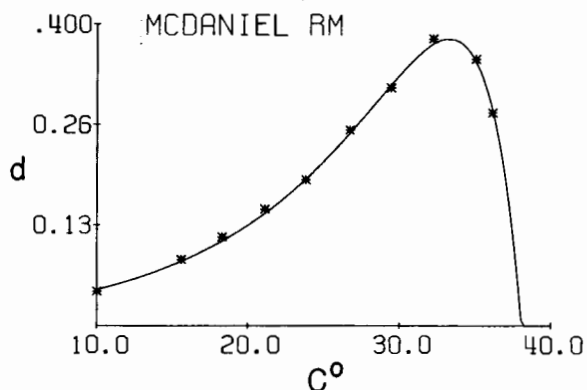


FIG. 6.—Instantaneous population growth rate as a function of temperature for *T. mcdanieli*.

Appendix

Knowledge of uniformly valid, asymptotic solutions that result from application of singular perturbation techniques to prototype equations may substantially aid researchers in many fields. One of the most basic problems in the natural sciences is the deduction of an optimal, closed form representation of a curve which provides the best fit for a data set. It is the aim of this Appendix to demonstrate such singular perturbation results for a particular model equation and then to show how these results were used to determine an appropriate analytic expression for temperature-dependent, biological processes. Equations A.1–A.13 establish the form of the inner and outer expansions, including the choice of scaling factor for the independent variable inside the boundary layer. Necessary conditions that these expansions must satisfy for matching are given in equations A.14–A.18. Parenthetically stated these conditions imply that as one passes from the inner to the outer solution, or from the outer solution to the inner, both solutions must approach the same limit. Nondimensional quantities of the general solution are related to specific temperature parameters in A.23–A.26. The equation for finding thermal optimum is given in A.27. And finally, equations A.28–A.32 are deductively used to expand initial results to include a more general description.

Consider the following boundary value problem for $y = y(x; \epsilon)$;

$$\epsilon \frac{d^2y}{dx^2} + \frac{dy}{dx} + b_0y = 0, \quad 0 < x < 1, \quad 0 < \epsilon \ll 1; \quad (A.1a)$$

$$y(0, \epsilon) = 0, \quad y(1; \epsilon) = 1, \quad (A.1b)$$

where all quantities in (A.1) are assumed to be non-dimensionalized and b_0 is a positive constant. We wish to determine the lowest order approximation for the solution $y(x; \epsilon)$, which is uniformly valid in x for ϵ small. Although we could accomplish this by solving the problem exactly and then examining the asymptotic behavior of that solution for ϵ small, it is more advantageous to employ the following procedural technique that does not depend upon explicitly knowing the exact solution.

We first assume y , dy/dx , d^2y/dx^2 are of $O(1)$ as $\epsilon \rightarrow 0$ for $x \in I$ where I is an interval flanking $x = 1$ (later in this Appendix we demonstrate what happens if I were chosen such that it flanks $(x = 0)$). Then, since we are seeking a one-term approximation, we look for a solution to (A.1) of the form $y(x; \epsilon) = y_0(x) + O(\epsilon)$ where $y_0^{(n)}(x)$

$$= O(1) \text{ for } x \in I \text{ as } \epsilon \rightarrow 0; n = 0, 1, \text{ and } 2. \quad (A.2)$$

Substituting (A.2) into (A.1a) and that boundary condition of (A.1b) evaluated at $x = 1$ and neglecting all terms of $O(\epsilon)$, we obtain the following 1st order differential equation and boundary condition for $y_0(x)$:

$$y_0' + b_0y_0 = 0, \quad y_0(1) = 1. \quad (A.3)$$

Since the differential equation satisfied by y_0 is only first order, it would be impossible for y_0 to satisfy a boundary condition at $x = 1$ and one at $x = 0$ simultaneously. This is a characteristic of singular perturbation problems. Solving (A.3) we obtain

$$y_0(x) = \exp[-b_0(x-1)], \tag{A.4}$$

which is usually referred to as the lowest order term of the outer expansion for $y(x; \epsilon)$.

We now wish to rescale our variables so that for $x \in I'$, and interval flanking $x = 0$, our new dependent variable and all derivatives of it with respect to our new independent variable will be of $O(1)$ (Segel 1972) as $\epsilon \rightarrow 0$. That is we define

$$\xi = x/\delta(\epsilon), \quad Y(\xi; \delta) = y(x; \epsilon), \tag{A.5}$$

such that where $\xi = O(1)$ as $\epsilon \rightarrow 0$, Y , $dY/d\xi$, and $d^2Y/d\xi^2$ are of $O(1)$ but $\neq 0$ as $\epsilon \rightarrow 0$. Since we wish $\xi = O(1)$ as $\epsilon \rightarrow 0$ for x about 0, this implies $\lim_{\epsilon \rightarrow 0} \delta(\epsilon) = 0$. Substitution of (A.5)

into (A.1a) and that boundary condition of (A.1b), evaluated at $x = 0$, yields the following problem for $Y(\xi; \delta)$:

$$\frac{d^2Y}{d\xi^2} + \left[\frac{\delta(\epsilon)}{\epsilon} \right] \frac{dY}{d\xi} + b_0 \left[\frac{\delta^2(\epsilon)}{\epsilon} \right] Y = 0, \quad Y(0; \delta) = 0, \tag{A.6}$$

upon division of the original transformed differential equation by ϵ/δ^2 . Due to the restrictions on $d^2Y/d\xi^2$, $n = 0, 1$, and 2 , imposed above, it is necessary that neither of the terms in brackets in (A.6) goes to ∞ as $\epsilon \rightarrow 0$, and that only one of them can go to 0 . Thus without loss of generality we need only examine the following two cases:

$$\text{either } \frac{\delta(\epsilon)}{\epsilon} = 1 \quad \text{or} \quad \frac{\delta^2(\epsilon)}{\epsilon} = 1. \tag{A.7a,b}$$

For (A.7a), $\delta(\epsilon) = \epsilon$ which implies $\delta^2(\epsilon)/\epsilon = \epsilon$, while for (A.7b) $\delta(\epsilon) = \epsilon^5$, which implies $\delta(\epsilon)/\epsilon = 1/\epsilon^5$. Since $1/\epsilon^5 \rightarrow \infty$ as $\epsilon \rightarrow 0$ this latter case must be rejected; hence we select $\delta(\epsilon) = \epsilon$.

Therefore we consider

$$\xi = x/\epsilon, \quad Y(\xi; \epsilon) = y(x; \epsilon), \tag{A.8}$$

and (A.6) becomes

$$\frac{d^2Y}{d\xi^2} + \frac{dY}{d\xi} + \epsilon b_0 Y = 0, \quad Y(0; \epsilon) = 0. \tag{A.9}$$

Since Y , $dY/d\xi$, $d^2Y/d\xi^2 = O(1)$ where $\xi = O(1)$ [i.e. $-x = O(\epsilon)$] as $\epsilon \rightarrow 0$, we are justified in looking for a solution in this region of the form

$$Y(\xi; \epsilon) = Y_0(\xi) + O(\epsilon) \quad \text{where} \quad Y_0^{(n)}(\xi) = O(1) \quad \text{as} \quad \epsilon \rightarrow 0; \quad n = 0, 1, \text{ and } 2. \tag{A.10}$$

Substituting (A.10) into (A.9) and proceeding as before, we obtain the following problem for Y :

$$Y_0'' + Y_0' = 0, \quad Y_0(0) = 0. \tag{A.11}$$

Solving (A.11) we obtain

$$Y_0(\xi) = C_0[1 - \exp(-\xi)], \tag{A.12}$$

where C_0 is a constant still to be determined. This is usually referred to as the lowest order term of the inner expansion or boundary layer of $y(x; \epsilon)$. Thus we now have

$$y(x; \epsilon) \sim \begin{cases} y_0(x) = \exp[b_0(x-1)] & \text{for } x \in I \text{ such that } x = O(1) \\ & \text{as } \epsilon \rightarrow 0. \\ Y_0(x/\epsilon) = C_0[1 - \exp(-x/\epsilon)] & \text{for } x \in I' \text{ such that } x = O(\epsilon) \end{cases} \tag{A.13}$$

We wish to find C_0 and shall do this by means of the intermediate limit technique of matching the inner and outer asymptotic expansions.

Consider (A.13) in conjunction with Fig. A.1. Recall that $y_0(x)$ is a valid asymptotic expansion for $x = O(1)$ while $Y_0(x/\epsilon)$ is a valid expansion for $x = O(\delta(\epsilon)) = O(\epsilon)$ as $\epsilon \rightarrow 0$. We introduce a $\theta(\epsilon)$ as depicted in Fig. A.1 such that

$$\epsilon < \theta(\epsilon) < 1 \quad \text{where} \quad \lim_{\epsilon \rightarrow 0} \theta(\epsilon) = \lim_{\epsilon \rightarrow 0} \epsilon/\theta(\epsilon) = 0. \tag{A.14}$$

We now define a variable $\sigma = x/\theta(\epsilon)$ and consider an interval I'' such that for $x \in I''$, $\sigma = O(1)$ but not zero as $\epsilon \rightarrow 0$ [i.e. $-x = O(\theta(\epsilon))$]. Since these x 's are intermediate between $x = O(1)$ and $x = O(\epsilon)$, one postulates in the limit as $\epsilon \rightarrow 0$ that both the inner and outer expansions are valid in this region and hence equal. That is,

$$\lim_{\substack{\epsilon \rightarrow 0 \\ \sigma = O(1)}} \left[y_0(x) \Big|_{x = \sigma\theta(\epsilon)} \right] = \lim_{\substack{\epsilon \rightarrow 0 \\ \sigma = O(1)}} \left[Y_0(x/\epsilon) \Big|_{x = \sigma\theta(\epsilon)} \right]. \tag{A.15}$$

Now upon use of (A.14), (A.15) yields the one-term matching condition

$$y_0(0) = \lim_{\xi \rightarrow \infty} Y_0(\xi). \tag{A.16}$$

Applying (A.16) to (A.13) we obtain

$$C_0 = \exp(b_0), \tag{A.17}$$

and therefore,

$$y(x; \epsilon) \sim \begin{cases} y_0(x) = \exp[-b_0(x-1)] & \text{for } x = O(1) \\ & \text{as } \epsilon \rightarrow 0. \\ Y_0(x/\epsilon) = \exp(b_0)[1 - \exp(-x/\epsilon)] & \text{for } x = O(\epsilon) \end{cases} \tag{A.18}$$

The outer expansion $y_0(x)$ is a good approximation to the exact solution except near $x = 0$, or in the boundary layer, where the inner expansion $Y_0(x/\epsilon)$ is the correct approximation. We can construct an asymptotic representation that is uniformly valid in the interval $x \in [0, 1]$ by adding $Y_0(x/\epsilon)$ to $y_0(x)$ and then subtracting their common part as

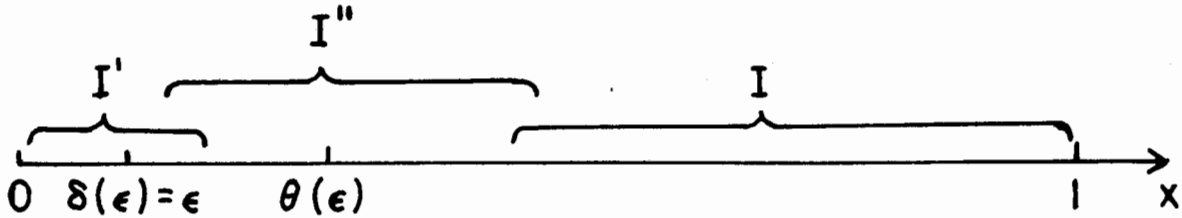


FIG. A.1.—A graphical depiction of the intervals I, I', and I'' as well as the scale factors $\delta(\epsilon) = \epsilon$ and $\theta(\epsilon)$ for the case of the boundary layer located at $x = 0$.

determined by the matching condition (A.16). This additive composite, which will be denoted by $y_u^{(0)}(x;\epsilon)$, has the general form,

$$y_u^{(0)} = y_0(x) + Y_0(x/\epsilon) - y_0(0); \quad (A.19)$$

or, for this case,

$$y_u^{(0)}(x;\epsilon) = \exp[-b_0(x-1)] + \exp(b_0)[1 - \exp(-x/\epsilon)] - \exp(b_0) = \exp(b_0)[\exp(-b_0x) - \exp(-x/\epsilon)]. \quad (A.20)$$

Finally we examine what would have occurred had we assumed that the boundary layer were located at $x = 1$. Then we would have found that

$$y(x;\epsilon) \sim \begin{cases} y_0(x) = 0 & \text{for } x \in I \\ & \text{such that } 0 \in I \\ & \epsilon \rightarrow 0, \\ Y_0(\eta) = A + (1-A)\exp(\eta) & \text{where } \eta = (1-x)/\epsilon \\ & \text{for } x \text{ in the boundary layer} \end{cases} \quad (A.21)$$

where A must be selected such that

$$y_0(1) = \lim_{\eta \rightarrow \infty} Y_0(\eta). \quad (A.22)$$

This will require that we choose A so that it satisfies

$$\lim_{\eta \rightarrow \infty} [A + (1-A)\exp(\eta)] = 0 \rightarrow A = 0 \text{ and } 1 \text{ simultaneously,}$$

which is, of course, impossible. It is a characteristic of the technique of matched asymptotic expansions that if one assumes the boundary layer to be located at the wrong end of the interval, it is impossible to fulfill the matching condition.

It remains only to relate these results to the problem at hand. Toward this end we introduce the following association between the nondimensional quantities of this Appendix and the relevant dimensional ones of the rate-temperature function:

$$\epsilon = \Delta T/T_M, \quad b_0 = \rho T_M, \quad x = 1 - T/T_M \quad \text{and} \quad y(x;\epsilon) = d(T)/\psi. \quad (A.23)$$

Then (A.18) transforms into

$$d(T) \sim \begin{cases} d_0(T) = \psi \exp(\rho T) & \text{for } T \text{ in Phase I} \\ d_1(\tau) = \psi \exp(\rho T_M)[1 - \exp(-\tau)] & \text{where } \tau = (T_M - T)/\Delta T \\ & \text{for } T \text{ in Phase II,} \end{cases} \quad (A.24)$$

with the implicit matching condition

$$d_0(T_M) = \lim_{\tau \rightarrow \infty} d_1(\tau). \quad (A.25)$$

Hence using (A.19) directly or transforming (A.20) with the aid of (A.23), we obtain the uniformly valid approximation

$$d(T) = \psi[\exp(\rho T) - \exp(\rho T_M - (T_M - T)/\Delta T)] \quad \text{for } T \in [0, T_M]. \quad (A.26)$$

It is now possible to determine a relationship between the optimum temperature T_0 , and the parameters of (A.23), namely

$$T_0 = T_M[1 + \epsilon \ln(\epsilon b_0) / (1 - \epsilon b_0)]. \quad (A.27)$$

We further pose the question of whether such a procedure as that illustrated in this Appendix can be used to provide new biological insights. In particular (A.1) has dimensional form

$$d'(T) = \rho d(T) + \Delta T d''(T), \quad d(0) = \psi, \quad d(T_M) = 0, \quad (A.28)$$

which has the physical interpretation that the change of rate with temperature is composed of a term (ρd) due to an effect on critical biochemical reactions and another ($\Delta T d''$) due to desiccation. If we modify (A.28) by including a nonlinear effect for enzyme heat denaturation, we obtain

$$d'(T) = d(T)[\rho - \gamma d(T)] + \Delta T d''(t), \quad d(0) = \psi, \quad d(T_M) = 0, \quad (A.29)$$

where $\gamma > 0$ is a denaturation constant. This would yield a modified outer solution satisfying

$$d_0'(T) = d_0(T)[\rho - \gamma d_0(T)], \quad d_0(0) = \psi; \quad (A.30)$$

or solving (A.30),

$$d_0(T) = \alpha [1 + k \exp(-\rho T)]^{-1} \quad \text{where } \alpha = \rho/\gamma \quad \text{and } k = \frac{\alpha - \psi}{\psi}. \quad (A.31)$$

The inner solution would remain the same and hence we could form a modified uniformly-valid, additive composite given by

$$d(T) = \alpha \{ [1 + k \exp(-\rho T)]^{-1} - [1 + k \exp(-\rho T_M)]^{-1} \exp(-\tau) \} \approx \alpha \{ [1 + k \exp(-\rho T)]^{-1} - \exp(-\tau) \} \quad \text{for } \tau = (T_M - T)\Delta T, \quad (A.32)$$

which should prove useful for modeling temperature-

dependent, rate phenomena which are sigmoid rather than exponential in the low temperature region.

Note that we have made the approximation in (A.32) that $d_0(T_M) \cong \alpha$, which is valid provided the line $T = T_M$ intersects the sigmoid curve, $d = d_0(T)$, at a point in the $T - d$ plane having an ordinate virtually identical in value to α , the horizontal asymptote of that sigmoid curve.

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