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Influence of Temperature Variations on Rate of Development in Insects: Analysis of Case Studies from Entomological Literature

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ABSTRACT Case studies on development-time data collected at constant and varying temperatures in a number of insects have been analyzed in a comparative manner to investigate the effects of temperature variations on rate of development. Sources of experimental errors are many and are not always adequately controlled. For statistical analysis, the more common problems include the assumption of a linear relationship between temperature and development rate over the whole temperature range and extrapolation or subjective vertical cutoff of the rate function in rate summation for varying temperatures. Development-time data of 26 species were selected for the analysis. For each species, the expected development time under each varying temperature regime was estimated by integrating constant temperature development rates over the 24-h varying temperature cycle. These estimates were then compared with the development times observed under the corresponding varying temperature regimes, and the significance of the differences was evaluated. The results as a whole suggest that the differences in development times between constant and varying temperatures could usually be accounted for by the effect of rate summation based on the curvilinear relationship between temperature and rate of development. The possible physiological mechanisms that act in addition to the rate-summation effect are briefly discussed. Finally, the need for more extensive and detailed investigations in this area of study is indicated.

KEY WORDS development rate, varying temperature, rate summation

THE RATES OF development in insects under natural conditions are largely determined by temperature. In most microenvironments, temperature is characterized by daily and seasonal cyclic variations with superimposed irregular fluctuations. However, studies of insect development rate most often involve experiments performed under constant temperatures (Howe 1967). In the development and application of development-rate models, it is always assumed that development rate at a given temperature is independent of thermal regime, whether the model is linear or nonlinear in relation to temperature. This assumption is also inherent in efforts to derive development-rate models from data obtained under varying temperatures, such as the work by Dallwitz & Higgins (1978). According to this assumption, development rate follows a definite function with respect to temperature, when other factors are equal, and the amount of development can be calculated by accumulating the fraction of development per unit time; i.e., rate summation (Kaufmann 1932). The procedure may be expressed as:

$$D = \int r[T(t)] dt \quad (1)$$

where development D is a function of temperature, T , which in turn is a function of time, t , and the development rate, r , adjusts instantaneously to temperature.

The above assumption is fundamental to the formulation of development-rate functions for phenological models. Attempts to study the validity of this assumption are numerous in entomological literature, and both positive and negative results have been reported (Hagstrum & Hagstrum 1970, Ratte 1984). In this article, we first offer a review of the methodology in this area of study, which points out that in many of the reports, investigative shortcomings exist in experimentation or data analysis, or both, and, thus, the significance of these reports needs to be established. We then use the development-time data of 26 species selected following a literature search, avoid the pitfalls in methods of data analysis, and carry out a comprehensive comparison of development times between constant and varying temperatures in these species. The objective is to determine whether there is any evidence for a physiological response, in a range of insects to varying temperatures, that acts in addition to the rate-summation effect.

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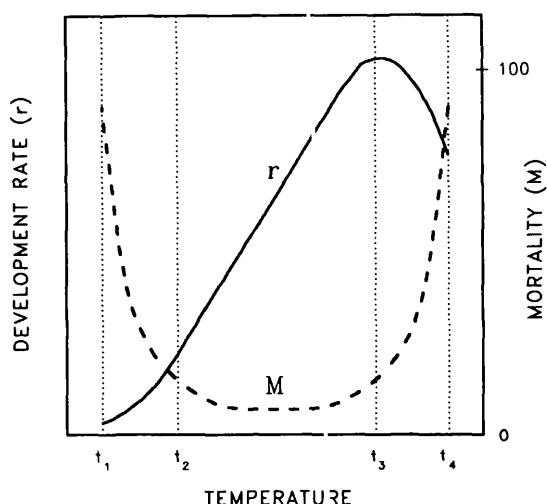


Fig. 1. Generalized functions of insect development rate and mortality under constant temperature.

Methodology

Effects of Varying Temperature. In studies of the effect of varying temperatures on rate of development, insects are reared at both constant and varying temperature regimes and the development rates at the two types of regime are compared. The varying regimes have various patterns. In this article, the square-wave pattern, consisting of a low and a high temperature with an abrupt transition between the two in a 24-h period, is referred to as *alternating temperature*. Smoothly changing, sine-curved pattern, again with a 24-h cycle, is referred to as *fluctuating temperature*. The term *varying temperature* is used to encompass both alternating and fluctuating temperatures.

It has long been recognized that development times of insects may differ, often considerably, between constant and varying temperature regimes with the same mean temperature (Hagstrum & Hagstrum 1970). There are two possible mechanisms for the differences observed. The first is, nonlinearity in the temperature-dependent rate function. The typical sigmoid curve relationship, as depicted in Fig. 1, has the corollary that, when temperatures fluctuate outside the middle (linear) range, development will be faster at low temperatures and slower at high temperatures when comparisons between constant and varying temperatures are made on the basis of daily mean temperatures (Tanigoshi et al. 1976). This is the consequence of the rate-summation effect, which can be feasibly taken into account by equation 1 in phenological models (Kaufman 1932, Worner 1992). The second is that temperature variation per se accelerates or decelerates development; that is, there is a physiological response that acts in addition to the rate-summation effect. Using the mathematical expression of equation 1, the second

mechanism means that the instantaneous rate at a given temperature is not independent of the temperature regime. If the second mechanism is operating with strong effects, then the $r(T)$ function will vary with the patterns of temperature variation and the difficulty of predicting development under natural conditions will be greatly increased. It is, thus, important to distinguish between the two mechanisms in studying the effects of varying temperatures on rate of development.

Analyzing the Effects of Temperature Variations. *Experimentation.* The comparison of development rates between constant and varying temperature regimes demands that the development times at both types of regimes have been determined with adequate accuracy. Many factors may influence the experimental precision. In particular, the following questions should be asked: Do the test cohorts actually experience the temperatures assigned to them? Are the test cohorts sufficiently homogeneous both within and between temperature treatments? Are the intervals of observation sufficiently short, and the sample sizes sufficiently large, for efficient estimations of mean development time (Shaffer 1983)? Because the study of any insect usually requires many temperature treatments across a time period, do all other influencing factors, such as nutrition and humidity, remain sufficiently equal both between treatments and across time? Howe (1967) offered a useful discussion of these and other factors. Experience shows that it is very difficult in practice to execute the required control on all the factors throughout the experiments. For instance, mean development times between replicates of the same temperature condition were observed to differ significantly or even obviously (Browning 1952, Butler 1966).

Development-Rate Curve Under Constant Temperature. When the rates of development and percentage of mortality of one or more immature stages of any species under a series of constant temperatures are plotted against these temperatures, a sigmoid curve for development rates and a U-shaped curve for mortality usually can be drawn, as shown in Fig. 1. For any species, there are both low and high temperature limits permitting complete development, which are designated as t_1 and t_4 , respectively. For most species, t_1 and t_4 space over a range of some 25°C across the temperature gradient between 5 and 40°C. Within the limits of t_1 and t_4 , the temperature range can be divided into the following three subranges: (1) t_1 – t_2 , development rate increases in an accelerating manner and mortality decreases rapidly, as temperature rises; (2) t_2 – t_3 , development rate increases more or less linearly with temperature and reaches its maximum at t_3 , and mortality rates are low and remain stable with respect to temperature; and (3) t_3 – t_4 , development rate decreases with temperature, and mortality rate increases rapidly and approaches 100% at t_4 .

It is seldom possible to prescribe the number of data points needed to derive the curve with the required precision, either by eye or mathematically. Howe (1967) suggests that the data points need to be spaced at temperature intervals of $\leq 2.5^\circ\text{C}$ for determining the position of the curve. For the purposes of this analysis, we used only data in which temperature intervals were $\leq 3^\circ\text{C}$ to derive rate functions.

Comparison of Development Rates Between Constant and Varying Temperature Regimes. In the literature, direct comparisons of mean development times or rates have often been made between constant and varying temperature regimes, which give the same mean daily temperatures (Messenger 1969, Hagstrum & Hagstrum 1970, Baker 1971, Hagstrum & Leach 1973, Yeargan 1980, Pak & Oatman 1982, Yeargan 1983). The results from such comparisons may be helpful to draw attention to the gross differences between the two types of regimes in their effects on rate of development. However, this method essentially mixes up the rate-summation effect and any additional physiological responses and, thus, should be abandoned in attempts to clarify the mechanisms of effects of varying temperatures on rate of development (Howe 1967, Worner 1992).

As discussed above, if the development rate at a given temperature is independent of thermal regime, then the development at varying temperature regimes can be estimated by the method of rate summation, as described in equation 1. In practice, equation 1 is approximated by rate summation over discrete time increments of <1 d:

$$D = \sum_{t=b}^e r[T(t)] dt \quad (2)$$

where b and e are the beginning and end of development duration under a given varying temperature regime. Thus, the fraction of development during each time increment is estimated by the constant temperature rate function, $r(T)$, and is summed up from 0 to 1. When D comes to be <1 or >1 , acceleration and deceleration of development by a physiological response that acts in addition to the rate-summation effect can be assumed.

The rate summation procedure of equation 2 has been used widely (Huffaker 1944, Messenger & Flitters 1959, Eubank et al. 1973, Tanigoshi et al. 1976, Liu & Hughes 1984, Liu & Meng 1989) but has not always been executed with due caution.

If one accepts that temperature intervals of $\leq 3^\circ\text{C}$ are the minimum requirement of the number of data points for determining an accurate $r(T)$ function at constant temperatures, then many of the $r(T)$ functions used for rate summation in the literature do not meet this minimum requirement over the whole or part of the temperature range under investigation (Munger & Cressman 1948, Fye et al. 1969, Hagstrum & Milliken 1991).

In other studies, extrapolations of $r(T)$ have often been boldly made in rate summation with equation 2. For example, in a study of development rates of *Tribolium castaneum* (Herbst), Hagstrum & Milliken (1991) conducted constant temperature experiments in the range of $22.5\text{--}35.0^\circ\text{C}$ and then extrapolated the rate function to the range of $17.5\text{--}40.0^\circ\text{C}$ in rate summation for varying temperature regimes. Similar exercises of extrapolation can be found in Eubank et al. (1973), Avilla & Copland (1988), and Fielding & Ruesink (1988). Estimations of development times with the aid of extrapolation can be useful in evaluating the predictive validity of a particular rate function derived from constant temperature data when used over a wider temperature range under varying regimes (see Hagstrum & Milliken 1991) but may offer spurious results if they are used to discern the mechanisms of temperature variations (Worner 1992).

Some studies use varying temperature regimes that include temperatures outside the low and high limits for complete development at constant temperature; i.e., t_1 and t_4 as defined in Fig. 1. In these circumstances, some authors assign rate values to the temperature extremes by extrapolation (Lin et al. 1954), while others simply assume that no development occurs outside the range of $t_1\text{--}t_4$ (Ludwig & Cable 1933; Harries 1943; Harries & Douglass 1948; Messenger & Flitters 1958, 1959; Yeargan 1980). This latter assumption is again unjustified, because it has been observed in many species that development can occur and accumulate under temperatures that fluctuate a few degrees $<t_1$ or $>t_4$, although no individual can complete its development when kept constantly at the temperature extremes (Headlee 1941, Harris 1943, Lin et al. 1954, Phelps & Burrows 1969, Luo & Li 1993, Morales-Ramos & Cate 1993).

As Howe (1967) has rightly pointed out, analysis of the effect of temperature variations on rate of development cannot be made unless the rate function for the constant temperature over the range of the varying regimes has been determined as precisely as possible. Although this requirement may be partially relaxed in studies where only selected alternating regimes are used for varying temperature and the required values of $r(T)$ in rate summation can be found directly from the original data points at constant temperatures (Harris & Douglass 1948, Siddiqui & Barlow 1972, 1973; Welbers 1975, Fielding & Ruesink 1988), it must be observed that no extrapolation of $r(T)$ should be allowed, and in any case the analysis must be restricted to the temperature range of $t_1\text{--}t_4$ (see Fig. 1).

There is one other problem associated with the application of equation 2. It is difficult to assign significance to the deviation of D from unity, because usually there are only few estimates of D for the species and the experimental errors can be substantial (see below). No statistical procedure

has been proposed for this purpose and, as a result, interpretations of the deviations have been made subjectively (Messenger & Flitters 1959, Eubank et al. 1973, Siddiqui & Barlow 1973, Tanigoshi et al. 1976). Perhaps some statistical procedure may be helpful when the data for large number of species have been appropriately grouped, as will be shown in the following sections of this article.

Materials and Methods

Data Collection. Data used in the current analysis were obtained from the published literature. Original data on the aphid parasite, *Diaeretiella rapae* (M'Intosh) (S.-S.L., unpublished data), were also used. Reports of studies of the effect of varying temperatures on rate of development are numerous and >100 selected articles were carefully examined in the literature search, but only a fraction provide suitable data. The three major requirements for inclusion of data into this analysis were the following: (1) individuals of a species were reared at a series of constant temperatures and at one or more varying regimes, and all temperatures were accurately controlled within $\pm 0.5^\circ\text{C}$ of the assigned values with other conditions, such as relative humidity and nutrition, being the same at all temperature treatments; (2) the intervals of observation were ≤ 1 SD of mean development time, and the number of individuals that completed development at a given temperature regime was ≥ 30 , so that the mean development time obtained is reliable (Shaffer 1983); and (3) in cases where a rate function for the constant temperatures is going to be derived mathematically with equation 3, the intervals of the constant temperatures were $\leq 3^\circ\text{C}$. In many reports, only the mean development times, but no statistics of variability were presented. To judge the reliability of the mean values in these reports, the regression equation $SD = 0.209x^{0.730}$ (Shaffer 1983) was used to estimate the value of standard deviation, which was then compared with the length of observation intervals. In some other reports, only the median development times were shown, median times are accepted in the analysis when the intervals of observation were $< 10\%$ of the respective median values. In all, data on 26 species in six families reported in 23 articles have been selected (Table 1).

The data in many other reports, although obtained and presented properly for their original purposes, cannot be included in the current analysis. For example, many articles presented part or all data graphically (e.g., Tanigoshi et al. 1976, Fan et al. 1992), other studies used varying temperature regimes other than a 24-h cycle (e.g., Ludwig & Cable 1933, Mellors & Bassow 1983). It should also be noted that in most of the 23 studies included in Table 1, only part of the data from each article was included in the analysis for reasons of data suitability. For example, in Messenger & Flitters (1959), the embryonic development times of

each of the three species of fruit flies (E, F, and G) were measured at 14–18 varying temperature regimes, but only the data at 6–7 regimes were suitable because other temperature regimes included temperatures $< t_1$ or $> t_4$ (see Fig. 1) or exhibited $\geq 0.5^\circ\text{C}$ differences between actual and assigned mean temperatures.

Curve Fitting for Constant Temperature Data. The nonlinear model developed by Sharpe & DeMichele (1977) and modified by Schoolfield et al. (1980) was chosen, because the model can provide an excellent description of development times over a full range of temperatures and can be modified easily to describe times over a portion of that range (Wagner et al. 1984). The model is expressed as:

$$r(T) = \frac{RH025 \frac{T}{298.15} \exp \left[\frac{HA}{1.987} \left(\frac{1}{298.15} - \frac{1}{T} \right) \right]}{1 + \exp \left[\frac{HL}{1.987} \left(\frac{1}{TL} - \frac{1}{T} \right) \right] + \exp \left[\frac{HH}{1.987} \left(\frac{1}{TH} - \frac{1}{T} \right) \right]} \quad (3)$$

where $r(T)$ is mean development rate at temperature $T(^{\circ}\text{K})$, and $RH025$, HA , TH , HH , TL , and HL are fitted parameters.

It has been shown recently by Kramer et al. (1991) that in fitting nonlinear temperature-dependent development models, parameters are evaluated more satisfactorily in terms of the observed time than in the modified form of rate. Thus, in the process of parameter evaluation, equation 3 was reparameterized as a time model by inverting the equation on both sides.

A BASIC program, based on the Marquardt techniques (Marquardt 1963), was developed to fit the model to various data sets (Table 2). In some cases, the article did not have a sufficient number of data points required by the six-parameter model, equation 3 was then modified by removing the first exponential term in the denominator to the form of a four-parameter model (Wagner et al. 1984).

In many studies with alternating temperature regimes, the $r(T)$ values needed for rate summation can be found directly from the observed data under constant temperatures (e.g., species A, C, and H in Table 1), curve fitting for constant temperatures is not required and the analysis can be made even only a few data points are available for the constant temperatures.

Simulation of Fluctuating Temperatures. In studies with fluctuating regimes, temperature changes were usually programmed to a sine-wave pattern. Thus, in the following calculations, temperatures in fluctuating regimes were assumed to change sinusoidally over a diurnal range around the mean temperature:

$$T(t) = (\text{Max} - \text{Min})/2 \times \sin(2\pi t/24) + (\text{Max} + \text{Min})/2 \quad (4)$$

Table 1. Sources and ranges of data of effects of temperature variations on development rates of different species and stages of insects and the results of comparison between observed and predicted development times at varying temperatures

Code	Species	Stage	Range of constant temp, °C	Varying temp		No. test	$\bar{d} \pm \text{SEM}$	t^b	Source
				Type	Range ^a				
Coleoptera									
A	<i>L. oregonensis</i>	Egg	10.0–32.3	a	18.3–29.4	1	–5.266		Simonet & Davenport 1981
B	<i>T. castaneum</i>	Total	22.5–35.0	f	22.5–35.0	2	5.114 \pm 3.697		Hagstrum & Milliken 1991
C	<i>Tribolium confusum</i>	Egg	17.0–40.0	a	17.0–25.0	6	8.330 \pm 0.481	17.315**	Lin et al. 1954
		Egg	20.0–30.0	a	20.0–30.0	4	–15.566 \pm 4.417		Mikulski 1936
		Pupa	22.5–30.0	a	22.5–30.0	2	–15.758 \pm 7.264		Mikulski 1936
Diptera									
D	<i>Anopheles quadrimaculatus</i>	L–P	15.1–34.6	a	19.0–32.5	10	5.719 \pm 2.681	2.133	Huffaker 1944
E	<i>Ceratitis capitata</i>	Egg	12.2–35.0	f	12.2–35.0	6	1.074 \pm 1.827	0.588	Messenger & Flitters 1958, 1959
F	<i>Dacus cucurbitae</i>	Egg	12.2–35.6	f	12.2–35.6	7	–1.939 \pm 3.673	0.528	Messenger & Flitters 1958, 1959
G	<i>D. dorsalis</i>	Egg	13.9–36.1	f	13.9–36.1	7	–0.433 \pm 1.231	0.352	Messenger & Flitters 1958, 1959
H	<i>Drosophila melanogaster</i>	Total	15.0–27.5	a	15.0–27.5	5	2.166 \pm 1.903	1.138	Siddiqui & Barlow 1972
I	<i>Exorista mella</i>	E–L	15.0–30.0	a	15.0–30.0	1	–2.121		Butler et al. 1968
		Pupa	15.0–30.0	a	15.0–30.0	1	15.649		Butler et al. 1968
Hemiptera									
J	<i>Oncopeltus fasciatus</i>	Egg	15.0–35.0	a	16.0–25.0	8	0.755	1.385	Lin et al. 1954
K	<i>Anas tristris</i>	Nymph	21.1–35.0	a	21.1–32.2	1	0.846		Fielding & Ruesink 1988
Homoptera									
L	<i>Acyrthosiphon pisum</i>	Nymph	5.0–25.0	a	5.0–25.0	4	5.215 \pm 2.251		Siddiqui et al. 1973
M	<i>C. tenellus</i>	Egg	15.5–40.6	a	15.5–37.8	17	4.711 \pm 0.603	7.813**	Harris & Douglass 1948
		Nymph	18.3–40.6	a	18.3–37.8	9	8.342 \pm 1.227	6.799**	Harris & Douglass 1948
N	<i>L. erysimi</i>	Nymph	8.3–35.1	a	8.3–35.1	8	2.303 \pm 0.973	2.367*	Liu & Meng 1989
		Nymph	6.2–30.0	f	10.1–33.5	2	1.115 \pm 3.095		Liu & Meng 1989
O	<i>M. persicae</i>	Nymph	6.2–30.0	a	6.2–30.0	7	1.382 \pm 1.976	0.699	Liu & Meng 1989
		Nymph		f	6.0–30.0	2	0.890 \pm 3.561		Liu & Meng 1989
Hymenoptera									
P	<i>D. rapae</i>	Total	14.2–26.2	a	14.2–22.5	1	–2.119		Liu (unpublished)
Q	<i>Trichogramma confusum</i>	Total	14.0–35.0	a	20.0–30.0	1	–0.234		Liu et al. 1988
R	<i>T. denrolimi</i>	Total	20.0–34.0	a	20.0–34.0	3	1.947 \pm 0.719		Wu et al. 1994
S	<i>T. pretiosum</i>	Total	15.0–34.0	f	15.0–34.0	3	0.685 \pm 0.358		Butler & Lopez 1980
Lepidoptera									
T	<i>Amagastia kuehniella</i>	Total	20.0–27.5	a	20.0–27.5	3	–2.456 \pm 0.404		Siddiqui & Barlow 1973
U	<i>Diaphania indica</i>	Pupa	26.0–36.0	a	26.0–36.0	4	0.067 \pm 0.926		Wu et al. 1994
V	<i>Heliothis zea</i>	Egg	21.1–35.0	f	21.1–35.0	5	–1.101 \pm 1.266	0.870	Eubank et al. 1973
W	<i>Pectinophora gossypiella</i>	Total	18.0–34.0	a	18.0–34.0	3	3.203 \pm 2.890		Welbers 1975
X	<i>Pseudaletia unipunctata</i>	Egg	10.0–31.0	a	13.0–29.0	2	–0.934 \pm 2.769		Guppy 1969
		Larva	13.0–29.0	a	13.0–29.0	2	0.814 \pm 4.046		Guppy 1969
Y	<i>Spodoptera exigua</i>	Egg	23.9–35.0	a	23.9–35.0	1	0.397		Butler 1966
		L–P	23.9–35.0	a	23.9–35.0	1	0.726		Butler 1966
Z	<i>Spodoptera frugiperda</i>	Total	18.3–35.0	a	21.1–32.2	1	3.745		Barfield et al. 1978

a, Alternating; f, fluctuating; L–P, larva–pupa; E–L, egg–larva.

° Temperature range within which the data allow valid comparison.

° T values for the deviation of \bar{d} from unity for species that have five or more estimates of d. *, $P < 0.05$; **, $P < 0.01$.

Table 2. Estimates of parameters for equations describing relationship between temperature (K) and development times for nine species of insects at constant temperatures

Code	Species	Stage	RH025	HA	TH	HH	TL	HL	n	R ²	Relative deviation (%) ^a Mean \pm SD
B	<i>T. castaneum</i>	Total	0.0404	48,464	299.6	49,415			6	0.9984	2.05 \pm 1.82
D	<i>A. quadrimaculatus</i>	L-P	0.2084	37,123	298.0	45,516			7	0.9968	2.30 \pm 2.13
E	<i>C. capitata</i>	Egg	0.0210	19,657	306.5	59,950	285.2	-64,401	17	0.9989	1.91 \pm 1.38
F	<i>D. cucurbitae</i>	Egg	0.0387	14,476	307.8	72,077	285.7	-56,047	18	0.9993	2.00 \pm 1.90
G	<i>D. dorsalis</i>	Egg	0.0378	1,573	310.0	212,337	294.0	-40,869	16	0.9996	0.68 \pm 0.51
N	<i>L. erysimi</i>	Nymph	0.2149	1,544	309.4	82,697	289.9	-35,282	12	0.9994	1.54 \pm 1.88
O	<i>M. persicae</i>	Nymph	0.2090	12,965	303.4	72,545	279.4	-46,016	11	0.9995	1.87 \pm 1.83
S	<i>T. pretiosum</i>	Total	0.1162	21,656	305.7	56,775	285.9	-338,465	10	0.9992	1.89 \pm 1.65
V	<i>H. zea</i>	Egg	0.0142	18,245	307.3	45,945			6	0.9998	0.42 \pm 0.29

Development times of *C. capitata*, *L. cucurbitae*, *D. dorsalis*, and *H. zea* are in hours, otherwise development times are in days.

^a Deviation of the fitted curve from the observed values.

where T is temperature, t is the hour of day, and $t/24$ is the fractional part of the day, and Max and Min are the maximum and minimum daily temperatures. By definition $(\text{Max} - \text{Min})/2$ is the amplitude of temperature change, while $(\text{Max} + \text{Min})/2$ is the daily mean temperature.

Calculating the Expected Development Times at Varying Temperature Regimes. Because the actual beginning and end of the development duration at each varying regime could not be found from the literature, equation 2 was modified to estimate the development rate per day, D_d ,

$$D_d = \sum_{t=0}^{24} r[T(t)] dt \quad (5)$$

where t is the hour of the day and $T(t)$ is the average temperature during that hour. The time increments of 1 h for rate summation were chosen by trial-and-error calculations, which showed that 1-h intervals gave estimates almost identical to those obtained with shorter time intervals (Table 3).

Calculations of D_d with equation 5 may differ in the ways the $r(T)$ values were derived. In 17 of the 26 species, $r(T)$ values were obtained directly from the development times observed at the respective constant temperatures, and the calculations were straightforward. For example, the eggs of *Listronotus oregonensis* (LeConte) (species A) hatched in 12.8 d at 18.3°C and in 4.8 d at 29.4°C and by taking the reciprocals of development times, it was

assumed that the eggs completed 0.3255% of development in 1 h at 18.3°C and 0.8681% in 1 h at 29.4°C. Thus, in 8 h at 18.3°C followed by 16 h at 29.4°C each day, the percentage of development per day D_d was calculated as $D_d = 0.3255\% \times 8 + 0.8681\% \times 16 = 16.49\%$. In the remaining nine species, $r(T)$ values were taken from the fitted curves for the constant temperatures (Table 2) and the rate summations were done with the aid of computer.

Once D_d is obtained, the expected mean development time, $D_e(V)$, is calculated as:

$$D_e(V) = 1/D_d \quad (6)$$

Comparison of Observed with Estimated Development Times. For each varying temperature regime, the deviation of $D_e(V)$ from the observed mean development time, $D_o(V)$, is calculated as:

$$d = [D_e(V)/D_o(V) - 1] \times 100 \quad (7)$$

where d is the percentage of deviation for which positive value indicates acceleration, while negative value indicates deceleration. If the development at varying temperatures can be accounted for by the rate-summation effect, the percentage of deviations should approach a normal distribution with a mean of zero when the number of tests (i.e., sample size) is sufficiently large. Thus, the Student's t -test is used to test the significance,

$$t = (\bar{d} - 0)/SE(\bar{d}) = \bar{d}/SE(\bar{d}) \quad (8)$$

Table 3. Comparison of development times at varying temperature regimes calculated by rate summation with various lengths of time intervals from 0.5 to 2.0 h

Species	Stage	Temp range, °C ^a	Range of percent deviation ^b			
			Amplitude, $\pm 5^\circ\text{C}$		Amplitude, $\pm 10^\circ\text{C}$	
			1.0-0.5 h	2.0-0.5 h	1.0-0.5 h	2.0-0.5 h
<i>D. cucurbitae</i>	Egg	12-36	-0.2-0.2	-0.9-0.3	-0.4-0.1	-1.7-0.3
<i>L. erysimi</i>	Nymph	8-35	-0.1-0.1	-0.6-0.5	-0.3-0.0	-1.6-0.0

^a Temperature range indicates the limits for minimum and maximum temperatures, so the ranges of daily mean temperatures are in much narrower ranges.

^b Because the shorter the time intervals used in the rate summation, the more accurate the results, the development times obtained with 0.5-h intervals are always used as the standard value to calculate deviations.

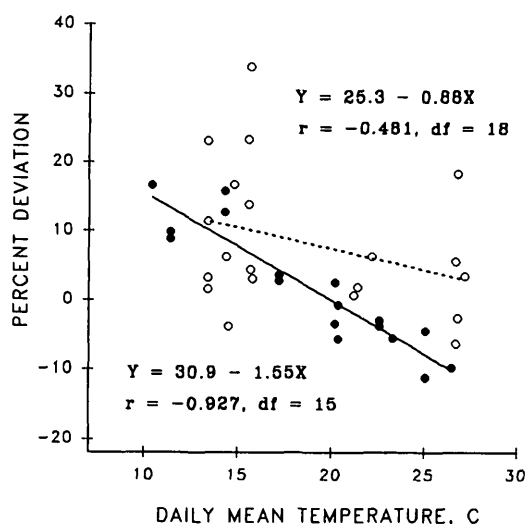


Fig. 2. Percent deviation of development times at constant temperatures from those at varying temperatures with the same mean. Depicted are the combined data for species E, F, and G (○) and the combined data of species N and O (●), respectively. The five species were chosen because their development times were measured in detail at constant and varying temperatures. The combinations of different species were permitted by the similar performances of species in each group.

when $|t| > t_{0.05}$, the deviation is significant. This significance test was first applied to the whole set of data of 26 species, to data of single species, and then to subsets of data grouped by insect taxa, by temperature ranges, and by types and amplitude of temperature variations to further test the effects of these factors.

Results

Whole Set of Data. The whole set of data includes 140 mean or median values of development times obtained at varying temperature regimes in 26 species (Table 1). When the development times between constant and varying temperature regimes are compared on the basis of mean temperatures, it is apparent that development at varying regimes is faster at low temperatures but slower at high temperatures, as is shown by the data in a few representative species depicted in Fig. 2. As discussed above, such a trend of difference along the temperature gradient may be expected from the rate-summation effect. The immediate query is whether the rate-summation effect accounts for all the differences or a possible physiological mechanism may act additionally.

Parameters of Constant Temperature Rate Function. Table 2 presents the least-square estimates of parameters of equation 3 for the nine species in which the fitted $r(T)$ curves were used in the rate summation. The goodness-of-fit of the model to the data in each species is shown by its

coefficient of determination, R^2 , and by the relative deviations of the model values from the observed development times. It can be seen that in every species the model fits the data very well.

Significance Test for the Whole Set of Data. By using equations 5, 6, and 7, the percentage of deviation, \bar{d} , was calculated for each of the 140 varying temperature regimes. The results are presented graphically in Figs. 3 and 4.

In 23 of the 26 species, deviations of $D_e(V)$ from $D_o(V)$ lie mostly within $\pm 5\%$ (Fig. 3). In species C, D, and M, the deviations are usually much greater (Fig. 4). However, in species C, the positive and negative deviations were reported separately by two groups of authors (Table 1). In species D, both positive and negative deviations are commonly exhibited by pairs of similar varying temperature regimes, indicating that the experimental errors were substantial. Such large experimental errors were also exhibited in data for some other species. For example, in species F, varying temperature regimes with a mean of $\approx 15^\circ\text{C}$ and an amplitude of $3\text{--}6^\circ\text{C}$ resulted in deviations from -18 to $+11\%$ (Fig. 3).

When the data for the 26 species were combined, the mean deviation, \bar{d} , was significantly higher than zero. However, \bar{d} became insignificant when the data of species M were excluded (Table 4).

Significance Test for Single Species. Significance test of the mean deviation, \bar{d} , was applied to each of the 10 species in which five or more values for \bar{d} were obtained for a single stage (Table 1). In 3 of the 10 species, the deviations are significant. However, the significance for species C must be accepted with caution, because the deviations obtained by another researcher were contradictory (Table 1).

Significance Test for Different Taxa. To reveal the possible differences between insect taxa, the data were divided by orders of insects and the significance test was applied to the subsets of data in each order. In five of the six orders, the deviations are not significant. In Homoptera, \bar{d} is significantly higher than zero, and this remains true even when the data of species M are excluded (Table 4).

Significance Test for Temperature Ranges. Because insect species may differ greatly in their requirements of temperatures favorable for development (Ratte 1984), the effects of temperature ranges can probably be demonstrated best in terms of their favorableness to development in each species rather than by the actual values of temperature. For the purpose of this analysis, the temperature range of $t_1\text{--}t_4$ is divided into three subranges, as shown in Fig. 1. When a sufficient number of constant temperature treatments have been conducted, the temperatures of t_1 and t_4 can be spotted from the original data. For example, from data by Messenger & Flitters (1958), the temperatures of t_1 and t_4 may be comfortably assumed to be 12.0

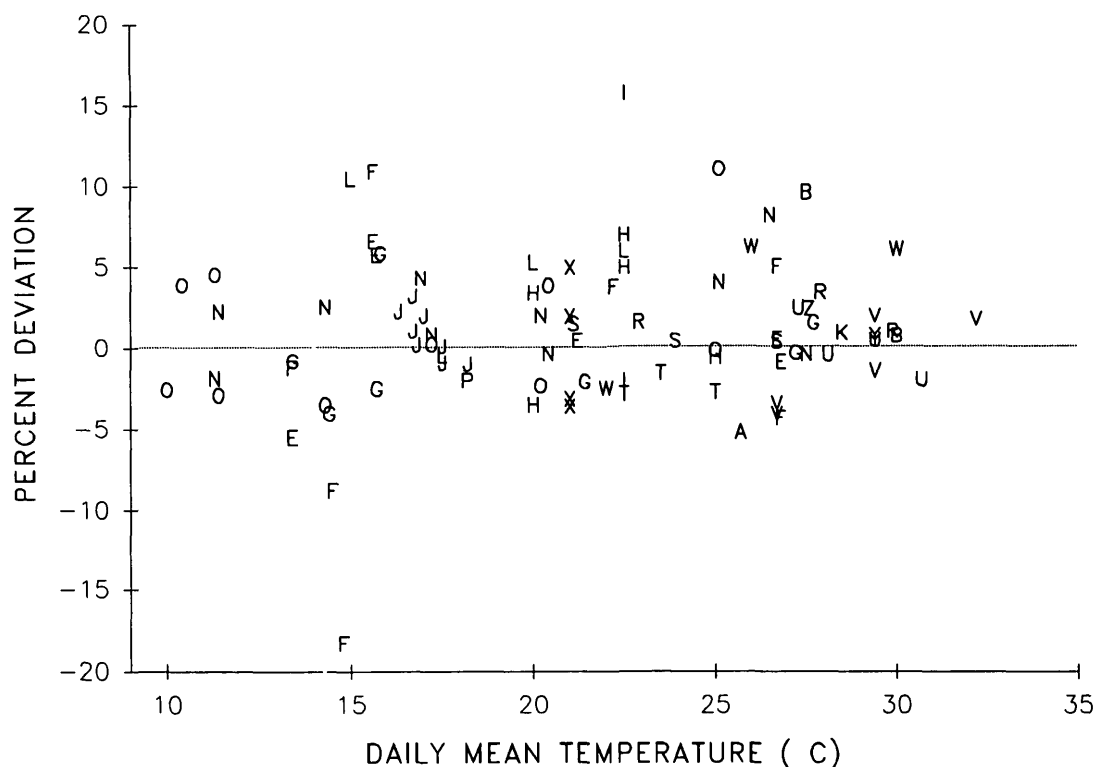


Fig. 3. Percent deviations of predicted from observed mean development times at varying temperature regimes as a function of temperature in 25 species of insects. Each letter represents the result of one varying temperature regime, and different letters represent different species as coded in Table 1. See text for description of method for comparison.

and 35.5°C, 11.5 and 36.0°C, and 13.0 and 36.0°C for species E, F, and G, respectively. Division of t_1 - t_4 into subranges is more subjective. In this analysis, the values of t_2 and t_3 in each species were estimated as $t_2 = t_1 + t_s$, $t_3 = t_4 - t_s$ where $t_s = (t_4 - t_1)/5$.

Because determination of t_1 and t_4 requires treatments over the whole range of temperature permitting complete development under constant conditions and especially treatments of narrow temperature intervals around the limits, the determination could be done in only seven species in two orders (Table 5). In each of the seven species, the varying temperature regimes were grouped according to their positions across the subranges into three categories of t_1 - t_3 , t_2 - t_3 , and t_2 - t_4 (see Fig. 1). Because there were only fewer than four trials for varying temperatures in each subrange of temperature in each species, the data for all species in each order were combined to test their significance.

The results in Table 5 show that in the four species of Diptera, no significant effect was found for temperature ranges. However, in the three species of Homoptera, varying temperature regimes in the range of t_2 - t_4 , i.e., including high temperatures above t_3 , produced positive deviation, suggesting a

possible physiological response that acts in addition to the rate-summation effect to bring about acceleration of development.

Significance Test for Patterns of Temperature Change. The whole data set was divided into subsets by types and amplitude of temperature variations (Table 6). In this part of the analysis, the data of both species C and M were excluded, because the data for species C were contradictory between the two reports and the data of species M showed consistent accelerative effect by temperature variations. The results in Table 6 suggest that alternating regimes with amplitude $\geq 5^\circ\text{C}$ are more likely to produce a physiological response that acts in addition to the rate-summation effect to bring about acceleration of development. However, this indication of acceleration is partly overlapping with effect of temperature range shown in Table 5, because this subset of data included seven of the eight trials for Homoptera in the temperature range of t_2 - t_4 .

Discussion

Development times between constant and varying temperatures with the same mean differ in a general pattern (Fig. 2, see also Hagstrum

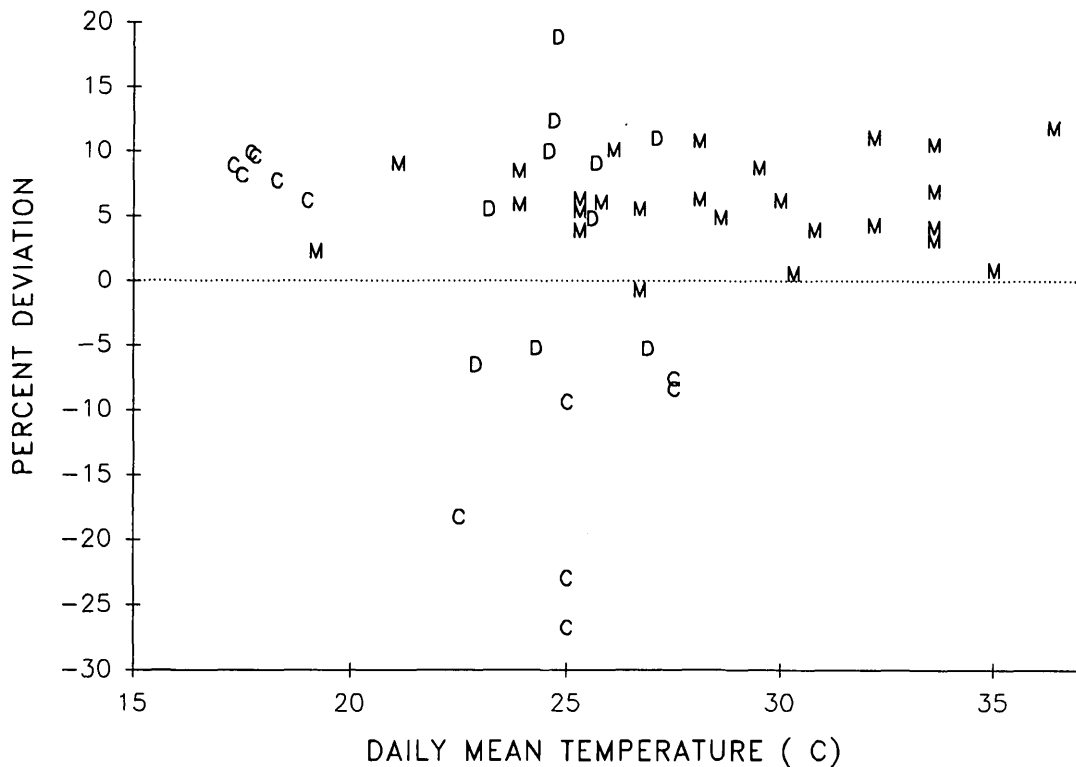


Fig. 4. Percent deviations of predicted from observed mean development times at varying temperature regimes as a function of temperature in three species of insects. Each letter represents the result of one varying temperature regime, and different letters represent different species as coded in Table 1. See text for description of method for comparison.

& Milliken 1991). However, when the expected development times at varying temperatures were calculated by rate summation, there were no consistent and significant deviations of the estimated from observed values except in rare cases. In this study, great care has been taken to ensure that the rates used in estimating the development times at varying temperatures were determined accurately at constant temperatures or, where a rate function is used, the function has been determined as precisely as possible. As a

whole, the results suggest little evidence of physiological mechanisms that act in addition to the rate-summation effect. Influence of such physiological mechanisms, if present, must be slight and, thus, probably can be ignored in rate functions for phenological models in most cases, because the estimated development times were in general very close to the values observed at varying temperatures. This recommendation seems even more reasonable if one sees that development of insects can also be significantly affected

Table 4. Percentage of deviations of predicted from observed development times at varying temperatures and their statistical significance

Species category ^a	No. species	% deviations			
		<i>n</i>	$\bar{d} \pm \text{SEM}$	<i>t</i>	<i>p</i> ^b
All species	26	140	1.7129 \pm 0.5600	3.059	<0.005
Exclude M	25	114	0.8327 \pm 0.6280	1.326	NS
Coleoptera	3	15	-2.5904 \pm 3.2735	0.791	NS
Diptera	6	37	1.8430 \pm 1.2073	1.526	NS
Hemiptera	2	9	0.7655 \pm 0.4812	1.591	NS
Homoptera	4	49	4.1881 \pm 0.6104	6.861	<0.001
Exclude M	3	23	2.3008 \pm 0.8558	2.689	<0.05
Hymenoptera	4	8	0.6934 \pm 0.5562	1.246	NS
Lepidoptera	7	22	0.0108 \pm 0.6674	0.016	NS

^a Single capital letters are codes of species listed in Table 1.

^b NS, not significant.

Table 5. Percentage of deviations of predicted from observed development times within different temperature ranges at varying temperatures in seven species of insects

Species category ^a	No. species	Temp range ^b	% deviations			
			<i>n</i>	$\bar{d} \pm \text{SEM}$	<i>t</i>	<i>P</i>
Diptera: E, F, G, H	4	t_1-t_3	13	-1.1508 ± 2.0983	0.548	NS
		t_2-t_3	9	2.0110 ± 1.1701	1.719	NS
		t_2-t_4	3	-0.8224 ± 1.8153	0.453	NS
Homoptera: L, N, O	3	t_1-t_3	8	1.2823 ± 1.6318	0.786	NS
		t_2-t_3	7	0.0453 ± 0.8176	0.055	NS
		t_2-t_4	8	5.2927 ± 1.1790	4.489	<0.01

^a Single capital letters are codes of species listed in Table 1.

^b For description, see Fig. 1 and text.

by some other factors, such as nutrition and humidity, whose effects are usually difficult to quantify precisely.

Physiological Mechanisms. The method of rate summation failed to account for all the deviations of those estimated from the observed values in Homoptera. In the beet leafhopper, *Circulifer tenellus* (Baker), there were consistent positive deviations (Fig. 4, species M). However, in the 26 species tested, this species appears rather unique in its response to varying temperatures.

Perhaps of more general significance is the acceleration of temperature in Homoptera when the insects are reared at varying temperature regimes in the range t_2-t_4 (i.e., the insects spend a portion of time each day at temperatures above t_3), brought about by a physiological response that acts in addition to the rate-summation effect. This finding suggests that such a physiological mechanism to bring about acceleration of development may exist in some insects but comes into play only within certain temperature ranges (also see Liu & Meng 1989, Liu, 1993).

Methodology. The problems in methodology have been discussed in detail above. With regard to the method of data analysis in this article, one may wonder that the results may be significantly shaped by the particular model used, because two

quite different models can fit a set of data equally well yet may provide different predictions (Worner 1992). In the development of analysis procedure used in this study, we initially compared the performance of three models, i.e., equation 3, Stinner four-parameter sigmoid model (Stinner et al. 1974, Kramer et al. 1991), and the Wang six-parameter sigmoid model (Wang et al. 1982, Liu & Meng 1989), in fitting the constant temperature data and estimating the expected development times at fluctuating temperatures in three species of insects. The three models were chosen for comparison by their wide differences in background assumptions and mathematical forms. The results in Table 7 show that in each of the three species the three models fit the data nearly equally well and offer very similar predictions for fluctuating temperatures by rate summation. It must be noted that we restricted the validity of the fitted $r(T)$ functions within temperature ranges examined experimentally. We also observed that in Worner's study (Fig. 4 of Worner 1992) significant disparity in predictions between her two models occurred only when extrapolations of $r(T)$ functions were allowed (i.e., mean temperatures $<15^\circ\text{C}$ or $>28^\circ\text{C}$). We concluded from Table 7 that, when the development time data at constant temperatures are spaced at intervals of $\leq 3^\circ\text{C}$, different sigmoid models will give very similar predictions within the experimental temperature range if the models can fit the data equally well. Therefore, choice of models, when appropriate, has little influence on the results.

For a number of species listed in Table 1, the current study has come to conclusions that differ from those by the original authors. For example, Messenger & Flitters (1959, p. 202) claimed that there were true accelerative effects by temperature variations in the three species of fruit flies (species E, F, and G), whereas, in fact, they assumed no development at temperatures $<t_1$ and $>t_4$ in estimations of development times for varying temperature regimes. So the true accelerative effects they claimed may be a direct result of this erroneous assumption.

Recently, Hagstrum & Milliken (1991) found that predictions of development times at varying temperatures were poor in some species even

Table 6. Percentage of deviations of predicted from observed development times within different types and amplitudes of varying temperatures in 24 species of insects

Type	Temp variation, $^\circ\text{C}$		No. species ^a	% deviations		
	Amplitude			$\bar{d} \pm \text{SEM}$	<i>t</i>	<i>P</i>
a and f	<5	16	58	0.7045 ± 0.4744	1.485	NS
	≥ 5	17	44	1.1792 ± 0.8310	1.339	NS
a	<5	12	42	0.6068 ± 0.4709	1.236	NS
	≥ 5	12	26	2.6456 ± 1.0701	2.593	<0.05
f	<5	6	16	0.9121 ± 1.0780	0.845	NS
	≥ 5	6	18	-0.7759 ± 1.4480	0.536	NS

^a The data of species C and M listed in Table 1 were excluded in the analysis, and the same species may appear in different categories.

Table 7. R^2 values for three species fitted to three S-shaped models and the comparative performance of the three models in making predictions of development time by rate summation over sinusoidally varying temperature regimes

Code	Species	Relative deviations (%) of predictions between models											
		Constant temp				Range of daily means of fluctuating temp, °C ^c	n^d						
		Temp range, °C ^a	R^2 of three models ^b					Stinner vs Sh-De		Wang vs Sh-De		Stinner vs Wang	
			Sh-De	Stinner	Wang			Mean	Max	Mean	Max	Mean	Max
F	<i>D. cucurbitae</i>	12–36	0.9993	0.9991	0.9996	17–31	15	−0.58	−1.00	−0.45	−1.77	−0.11	0.79
N	<i>L. erysimi</i>	8–35	0.9994	0.9993	0.9996	13–30	18	−0.25	−0.94	0.15	−0.60	−0.10	−0.37
S	<i>T. pretiosum</i>	15–34	0.9992	0.9989	0.9994	20–29	10	−0.16	−0.56	0.36	0.90	0.52	−1.46

^a Temperature range within which development times were measured experimentally at constant temperatures (see Table 1 for insect stages and sources of data).

^b Sh-De, Sharpe & DeMichele model (equation 3); Stinner, Stinner et al. (1974) four-parameter sigmoid model; Wang, Wang et al. (1982) six-parameter sigmoid model.

^c A fluctuating amplitude of $\pm 5^\circ\text{C}$ is considered in the predictions.

^d Predictions are made for each integer degree only which resulted in the number of predictions shown.

when the estimations were made by rate summation with $r(T)$ functions derived from rates measured at constant temperatures. However, because Hagstrum & Milliken (1991) made extensive extrapolations of the constant temperature rate functions in their predictions, their results were in part a reflection of the extrapolative behavior of the model used rather than any intrinsic differences between constant and varying temperatures.

In the data set included in the current study, many species were tested at only one or two varying temperature regimes within a limited range of temperature conditions. The results obtained for Homopterous species indicate that the effect of temperature variations may vary depending on the range of temperature. Furthermore, in the only species (species C) that has been investigated in some detail by two groups of authors, contradictory results were obtained (Mikulski 1936, Lin et al. 1954). Thus, the general conclusions drawn from this study must be accepted as preliminary and the effects of varying temperatures on rate of development in insects certainly merit more extensive experimental analysis.

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