

## INSECT POPULATION STUDIES.

### IV. DYNAMICS OF TEMPERATURE EFFECT ON INSECT DEVELOPMENT.

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### I. INTRODUCTION.

The problem of temperature effect on organic development is of so much theoretical interest for biologists in general and of so great practical economic importance for applied biologists, specially entomologists, that innumerable investigators have devoted their attention to this problem; still it has remained unsolved. This fact will be clear from the recent remarks of Wigglesworth (1942): 'This curve (of intensity or velocity of development) represents the sum or resultant of an immense number of chemical and physical reactions, many of which must be differently affected by changes of temperature. But in spite of this, numerous attempts have been made to describe these curves by simple equations. Such formulae can be made to fit particular cases and to that extent they have some descriptive value, but none of them is of sufficiently general application to be regarded as embodying any rational principle.' The present paper is meant to put forward a far clearer conception of this phenomenon than what has been held or reported so far. Of course it is by no means claimed that a complete solution of the problem has been achieved. In fact some further elaboration and modification of the findings presented herein are in view but the present contribution is being sent for publication as it marks the completion of a definite stage in the progress of our investigation.

At the first sight the paper may look to be too mathematical for a biological reader, but in fact it is not so. As far as possible effort has been made to keep all difficult mathematical portions out of the main body of the paper so that they may not interrupt a biological reader. The equations, which appear in the text, stand there as mere statements of facts, their derivation, etc. being given either in the footnote or in the appendices. This segregation of mathematical and biological language may also help a mathematical reader who may like to check up the purely mathematical derivations before concentrating on their biological interpretations.

II. DEDUCTION OF EQUATION.

In a previous communication (Pradhan, 1945) I have stated that the value of developmental index (reciprocal of developmental period like egg period, larval period, pupal period, etc.) of *Earias fabia* corresponding to any constant temperature is given accurately by the equation:

$$y = y_0 e^{-ax^2} \dots \dots \dots (I)^*$$

In that and a later communication (Pradhan, 1946) I have also shown how useful this equation is for tackling problems of fluctuating temperatures of the field. Now the following paragraphs are meant to show how we logically arrive at this equation, what physical meaning it carries or in other words which biophysical processes it symbolises.

The dynamics of development becomes crystal clear if we consider the following simplest case of hypothetical development: Suppose the single cell of a zygote begins to divide. Now if the daughter cells maintain their power of division unhampered and the development goes on constantly with a speed of one division per minute then we shall have:

TABLE I.

After 1st division or at the end of	1st minute	2 cells or	2 <sup>1</sup> cells.
.. 2nd	..	.. 4	.. 2 <sup>2</sup> ..
.. 3rd	..	.. 8	.. 2 <sup>3</sup> ..
.. 4th	..	.. 16	.. 2 <sup>4</sup> ..
.. 5th	..	.. 32	.. 2 <sup>5</sup> ..

and so on.

It is clear from the above example that although the speed of division, i.e., the number of divisions per minute, remains constant the amount of growth (i.e., the addition of cells) during successive minutes does not remain constant and increases in geometrical progression, i.e., *in accordance with the law of compound interest*.

Again if the time is fixed, say, one minute and the speed of division, i.e., the number of divisions per minute, is increased in some way then we shall have growth as depicted below.

TABLE II.

Speed of cell division.	Amount of development in a fixed period.
1 division per minute	2 cells or 2 <sup>1</sup> cells at the end of 1 minute.
2 divisions per minute	4 " 2 <sup>2</sup> " " 1 "
3 " " "	8 " 2 <sup>3</sup> " " 1 "
4 " " "	16 " 2 <sup>4</sup> " " 1 "
5 " " "	32 " 2 <sup>5</sup> " " 1 "

and so on.

It is clear from the above example that although the speed of cell division increases regularly in simple arithmetical progression, i.e., from 1 division per minute to 2, 3, 4 divisions per minute and so on, yet the speed of development, i.e., the amount of growth per minute (addition of cells), increases again in geometrical progression, i.e., *in accordance with the law of compound interest*, i.e., from 2 cells per minute to

\*  $y_0$  = highest value of developmental index.  
 $y$  = developmental index at temperature  $t^\circ$ .  
 $x$  =  $T - t$ .  
 $T$  = temperature corresponding to  $y_0$ .  
 $e$  = constant = 2.718282.

4, 8, 16 cells per minute and so on. Now based on the above examples we can write down the generalised equation

$$g = 2^n \quad \dots \quad (1)$$

A more accurate form of the above Equation 1 is

$$g = e^n \quad \dots \quad (2)^1$$

because according to the established mathematical fact, we take into account, by this modification, development at every moment and not only at the time of cell division.

Now if the total amount of growth ( $G$ ), which is required to complete the full development under consideration, is taken to be constant, then it can be shown mathematically <sup>2</sup> as well as it is easily comprehensible that if the value of ( $n$ ), i.e., the speed of cell division, is somehow increased, then the period required for full development, i.e., the developmental period, will correspondingly decrease and *vice versa*.

After understanding so far, another point has to be considered, namely, that the cell division is not the primary-most activity in organic development; cells do not remain simply dividing and redividing continuously but each cell after formation develops for a time and, so to speak, attains maturity before it is ready to divide again. Thus a cell's coming to maturity (when it is ready to divide) also marks the completion of a series of vital processes. This fact is best illustrated by a unicellular organism wherein there is no cell division except at the time of reproduction, but still development does continue from moment to moment. Therefore just as the speed of development of a multicellular organism, say up to maturity, can be expected to depend on the speed of cell division, similarly the speed of coming to maturity of single cells and hence the speed of cell division ( $n$ ) should depend on the speed of vital activities involved in the development and maturity of single cells. Hence if we suppose:

$$n = e^r \quad \dots \quad (3)$$

wherein ( $r$ ) is the speed of vital activities involved in the development of single cells and ( $n$ ) is the speed of cell division, then by substituting the value of ( $n$ ) in Equation 2 and taking a few mathematical steps <sup>3</sup> we easily come to

$$y = e^{e^r} \quad \dots \quad (4)$$

<sup>1</sup>  $g$  = speed of development, i.e., amount of growth (cell addition) which, however, goes on increasing in geometrical progression in successive units of time.

$n$  = number of cell divisions in unit time.

The equation should actually be written as

$g = Ke^n$  but for simplicity we take  $K = 1 = \text{a constant}$ .

<sup>2</sup> From Equation 2 we get (if  $P$  = developmental period and  $G$  = total development)

$$G = (e^n)^P = e^{n \cdot P} = \text{constant by hypothesis}$$

$$\therefore n \cdot P = \text{constant because } e = \text{constant}$$

or  $n \propto \frac{1}{P}$ , i.e., as the value of  $n$  increases the value of  $P$  decreases.

<sup>3</sup> Substituting the value of  $n$  from Equation 3 in Equation 2 we get

$$g = e^{e^r}$$

$$\therefore G = (e^{e^r})^P = \text{constant, if } P = \text{developmental period}$$

$$\text{or } G^{\frac{1}{P}} = e^{e^r}$$

$$\text{or } \log G^{\frac{1}{P}} = \log e^{e^r}$$

wherein ( $y$ ) is the developmental index, i.e., reciprocal of developmental period ( $1/P$ ).

It is clear from Equation 4 that the value of ( $y$ ) can increase only due to increase in the value of ( $r$ ), the value of ( $e$ ) being constant. Therefore the experimental fact that the value of ( $y$ ) increases with the rise of temperature shows that the speed of vital activities ( $r$ ) increases with the rise of temperature. Further, as shown by the so-called sigmoid curve of developmental indices, the rate of increase in the value of ( $y$ ) does not remain constant but remains continuously decreasing. These experimental observations show that a somewhat similar change might also be taking place in the value of ( $r$ ) with the rise of temperature. Now ( $r$ ) being the speed of activity a continuously decreasing rate of increase in its value reminds one of the principle of *retarded motion* and deeper thought on this comparison increases the probability of the two phenomena being absolutely similar. Therefore let us suppose for the time being as a trial that the value of ( $r$ )<sup>4</sup> increases with the rise of temperature but with a velocity which does not remain constant but which itself also remains getting retarded with the same rise of temperature; let us suppose the retardation to be uniform.

Now the sort of change in the value of ( $r$ ) as supposed above can be represented in mathematical language by the equations:<sup>5</sup>

$$v = u - at \quad \dots \dots \dots (5)$$

and

$$r = ut - \frac{1}{2} at^2 + c \quad \dots \dots \dots (6)$$

- Wherein  $v$  = resultant velocity of change in the value of ( $r$ ).  
 $u$  = a constant, i.e., value of ( $v$ ) when  $t = 0$ .  
 $a$  = retardation constant (i.e., negative acceleration).  
 $t$  = temperature.  
 $c$  = constant, i.e., value of ( $r$ ) when  $t = 0$ .

or  $\frac{1}{P} \log G = e^r$

or  $\frac{k}{P} = e^r$  because  $G$  or  $\log G =$  constant by hypothesis

or  $y = e^r$  if  $y = \frac{k}{P}$  where  $k =$  constant.

<sup>4</sup> This hypothesis must not be confused with what Janisch (1932) has written on pp. 150-158 applying the equation of retarded motion to the course of development.

<sup>5</sup> If a little change in the value of temperature is represented by  $dt$  and a corresponding change in the value of  $r$  by  $dr$  then

$$\frac{d^2r}{dt^2} = \text{acceleration} = -a \text{ by hypothesis}$$

$$\text{or } \int \frac{d^2r}{dt^2} dt = \int -adt$$

$$\text{or } \frac{dr}{dt} = v = -at + u, \text{ where } u \text{ is integration constant} \quad \dots \dots \dots (5)$$

$$\text{or } \int \frac{dr}{dt} dt = \int -at dt + \int u dt$$

$$\text{or } r = -\frac{1}{2}at^2 + ut + c, \text{ where } c \text{ is another integration constant} \quad \dots \dots \dots (6)$$

Further a few more mathematical steps <sup>6</sup> change the Equation 6 into

$$r = -\frac{1}{2}ax^2 + \log K \quad \dots \dots \dots (7)$$

wherein  $x$  represents the same quantity as it does in Equation I with which we started;  $K$  is a constant.

Then substituting the value of  $(r)$  from Equation 7 in Equation 4 we get <sup>7</sup>

$$y = Ke^{-\frac{1}{2}ax^2} \quad \dots \dots \dots (8)$$

and Equation 8 can be directly written as <sup>8</sup>

$$y = y_0 e^{-\frac{1}{2}ax^2} \quad \dots \dots \dots (9)$$

Now this Equation 9 is the same as Equation I which we started to arrive at except that  $(a)$  of Equation I is equal to  $(\frac{1}{2}a)$  of Equation 9.

Thus by simple presumptions and suppositions we arrive at an equation which is found to be promisingly applicable to what is supposed to be a complicated phenomenon, i.e., development as will be discussed further on.

### III. CURVE-FITTING AND TESTING GOODNESS OF FIT.

#### (a) Curve-Fitting.

As regards curve-fitting it must be made clear at the very outset that for fitting Equation I we cannot adopt the usual technique of fitting the frequency curves which a statistician might like to demand at the first sight due to a close similarity between Equation I and the equation of normal frequency curve. Neither we are dealing here with any distribution nor even our data represent a random sample of the total population of all the possible data. In fact our observations have been most systematically collected for definitely chosen points on the abscissa, i.e., the value of developmental periods and hence of developmental indices  $(y)$  have been determined for a few chosen values of temperature which actually are not chosen beyond a certain range due to very high pre-imaginal mortality at higher temperatures. Therefore despite the similarity referred to above, we have to resort not to the special method of fitting normal frequency curve but to the general method of

<sup>6</sup> Starting with Equation 6

$$\text{let } \frac{u}{a} = T \text{ or } u = aT, \text{ where } T \text{ is a constant both } u \text{ and } a \text{ being constants,}$$

and  $c + \frac{1}{2}aT^2 = \log K$ , where  $K$  is another constant (this constant  $K$  is different from  $K$  used in footnotes 1 and 3)

or  $c = \log K - \frac{1}{2}aT^2$ .

Substituting these values in Equation 6 we get

$$\begin{aligned} r &= -\frac{1}{2}at^2 + aTt - \frac{1}{2}aT^2 + \log K. \\ &= -\frac{1}{2}a(t^2 - 2Tt + T^2) + \log K. \\ &= -\frac{1}{2}a(T-t)^2 + \log K. \\ &= -\frac{1}{2}ax^2 + \log K \text{ if } x = T-t \quad \dots \dots \dots (7) \end{aligned}$$

<sup>7</sup> Substituting the value of  $r$  from Equation 7 in Equation 4 we get

$$\begin{aligned} y &= e^{-\frac{1}{2}ax^2 + \log K}. \\ &= Ke^{-\frac{1}{2}ax^2} \quad \dots \dots \dots (8) \end{aligned}$$

<sup>8</sup> Let the value of  $x = 0$  which is possible when  $t = T$  then,

$$y = Ke^0 = K.$$

Therefore  $K$  is the value of  $y$  when  $t = T$ , i.e., when  $x = 0$ , i.e.,  $K = y_0$ , i.e., the value of  $y$  when temperature is equal to  $T$  as explained in footnote \* on page 386.

fitting logarithmic curve after converting the exponential form into the polynomial form of equation. Thus Equation I is converted into<sup>9</sup>

$$Y = AX^2 + BX + C \quad \dots \dots \dots (10)$$

The values of the constants  $A$ ,  $B$ ,  $C$  can be determined simply by solving a set of normal equations.<sup>10</sup> The calculations involved in this solution are illustrated in Appendix A for ready reference. In Appendix B is given a modified form commonly known as the Doolittle method for solving these equations; this modification besides reducing arithmetical labour provides check for correctness of calculations at definite stages and also readily gives figures required to test the goodness of fit of the equation concerned (*vide infra*). Further the value of ( $a$ ) can be found out from Equation  $A = \frac{1}{2}a$  and the value of  $T$  from  $T = B/a$ . The value of ( $C$ ) gives the value of  $\log K$  and hence the value of ( $y_0$ ) by the equation  $C = \log K - \frac{1}{2}aT^2$ . Thus for example, by fitting the curve to the temperature effect on pupal periods of *Earias fabia* (*vide Appendix A*) we get

$$\frac{1}{2}a = .001107$$

$$T = 97.3$$

$$y_0 = 13.69.$$

Thus the equation comes to be

$$y = 13.69e^{-.001107(97.3 - t^{\circ}\text{F.})^2}.$$

Such equations for different sets of data are given in the beginning of each set in Table IV.

#### (b) Testing Goodness of Fit.

1. *Analysis of Variance Test.*—As regards testing goodness of fit of Equation 10 and thus of Equation I we can apply the exact statistical test by analysis of variance as illustrated in Appendix B in case we have individual observations to start with instead of average values of developmental periods corresponding to different constant temperatures as have been given by most of the previous investigators. We have applied this test to the case of nymphal periods of *Schistocerca gregaria* for which Hussain and Ahmad (1936) have fortunately published the individual observations. We find in this case as given below (Table III) that the fitness of Equation 10 is highly significant.

<sup>9</sup> Equation 9 which is the same as Equation I can be worked back to Equation 4 and then substituting the value of  $r$  from Equation 6 into Equation 4 we get

$$\begin{aligned} y &= e^{-\frac{1}{2}at^2 + ut + c}. \\ \text{or } \log y &= -\frac{1}{2}at^2 + ut + c. \\ \text{or } Y &= AX^2 + BX + C \\ \text{if } Y &= \log y. \\ A &= -\frac{1}{2}a. \\ t &= X \\ u &= B. \end{aligned}$$

<sup>10</sup> The equations referred to are

$$\begin{aligned} A\Sigma(X)^4 + B\Sigma(X^3) + C\Sigma(X^2) &= \Sigma(X^2 Y) \\ A\Sigma(X^3) + B\Sigma(X^2) + C\Sigma(X) &= \Sigma(X Y) \\ A\Sigma(X^2) + B\Sigma(X) + NC &= \Sigma(Y) \end{aligned}$$

$N$  being the number of observations and  $\Sigma$  being sign of summation.

TABLE III.  
Analysis of Variance.

Significance of degrees of freedom used in fitting Equation 10 to the logarithms of developmental indices of *Schistocerca* nymphs at different temperatures.

Degree of Fitting.	Description.	Sums of Squares.	D.F.	Variances.	Value of <i>F</i> .	
					Obs.	At 1%.
1	Total	1.87978	87			
	Regression	1.54781	1	1.54781	400.8	6.96
	Error	0.33197	86	0.00386		
2	Regression	0.29266	1	0.29266	636.2	6.96
	Error	0.03931	85	0.00046		

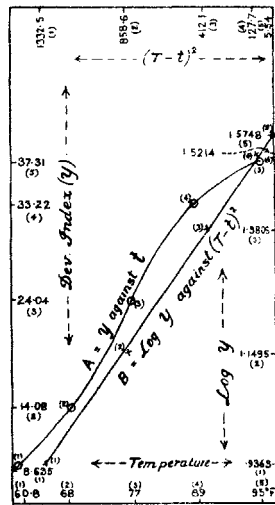
Conclusion.—Regression is highly significant.<sup>11</sup>

2. *Graphical Test.*—Coming to the graphical method of judging the suitability of curves, let us see what we should expect if Equation I correctly represents the relationship between developmental index and temperature. Equation I can be written as<sup>12</sup>

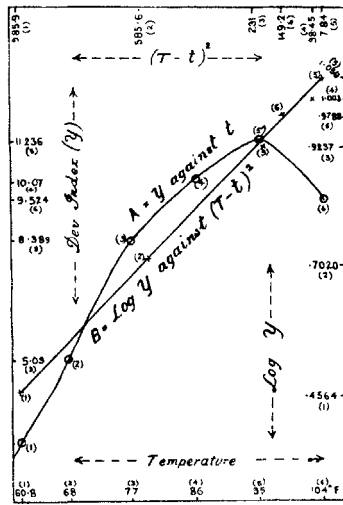
$$\log y = K_1 - AX^2 \quad \dots \dots \dots (11)$$

This Equation 11 shows mathematically that if Equation I correctly represents the relationship under consideration then we would get a parabola if  $\log y$  is plotted

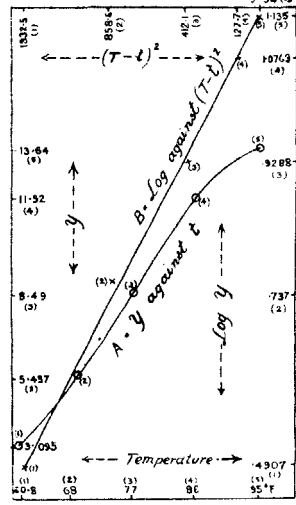
(1) *Earias* Egg-Periods



(2) *Earias*-Larval-Periods



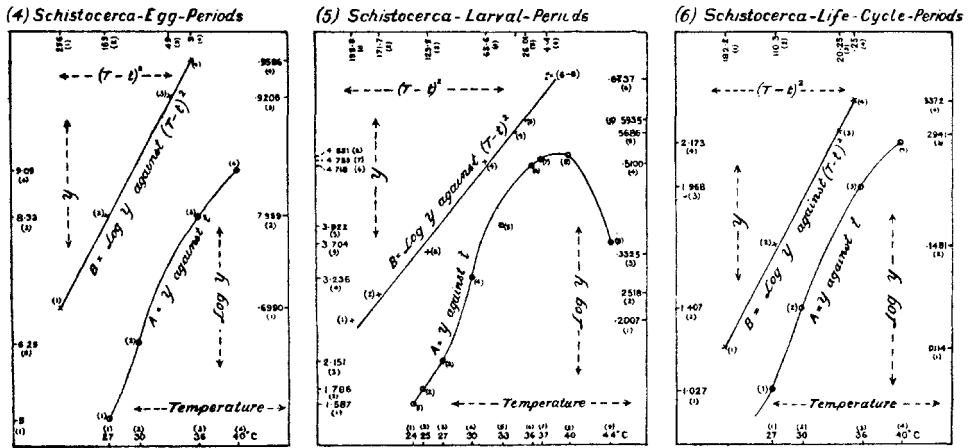
(3) *Earias*-Pupal-Periods



<sup>11</sup> We find in this case that variance due to an additional degree of freedom used in fitting a third degree curve is also significant showing that there may be some further gain in precision if a higher degree equation is used. This point, however, is in no way against the hypothesis of this paper and will be dealt with in detail in a subsequent publication.

<sup>12</sup> From Equation 7 we get  
 $\log y = \log y_0 - \frac{1}{2}ax^2$   
 or  $\log y = K_1 - AX^2 \dots \dots$  if  $K_1 = \log y_0$  and  $A = \frac{1}{2}a$ . (Parabolic relation)  
 or  $\log y = K_1 - AX_1 \dots \dots \dots$  straight line relation if  $X_1 = X^2$ .

against  $x$  and a straight line if  $\log y$  is plotted against  $x^2$  and Figs. 1 to 6 excellently satisfy this criterion. These six figures illustrate six different sets of data on developmental periods of different stages of two species of insects, namely, *Earias fabia* and *Schistocerca gregaria* belonging to orders Lepidoptera and Orthoptera respectively. The line  $A$  represents the curve obtained when  $y$  (developmental index) is plotted as ordinate against the abscissa of  $t$  (temperature) whereas line  $B$  is the graph obtained when  $\log y$  is plotted against  $X^2$ , i.e.  $(T-t)^2$ . It is instructive to note how all the observed points of the so-called sigmoid curve  $A$  arrange themselves along almost a clear straight line as demanded by the hypothesis of this paper. Figs. 2 and 5 illustrate this fact most prominently as in these figures the graph  $A$  exhibits greatest amount of curvature. Corresponding points of observation are serially numbered along both  $A$  and  $B$  as well as along scales of ordinate and abscissa. It should be noted that even points 6 and 9 of curve  $A$  in Figs. 2 and 5 respectively have come back to the same straight line in graph  $B$ .



It may also be interesting to remember at this stage that the advocates of the hyperbolic relation between temperature and insect development try to find a straight line in graph  $A$  itself.

3. *Agreement between theory and observation.*—Having determined the values of the constants of Equation I as given before we have calculated with its help the developmental periods corresponding to different temperatures and compared the same with observed values from ten different sets of data on various stages of three species of insects, two of which are the same as mentioned in the last section and the third is *Microbracon lefroyi* of order Hymenoptera. These calculated and observed values are given in Table IV and it will be found that the agreement is excellent. The observed values both for Figs. 1 to 6 and of Table IV were taken from already published papers of other workers—those for *E. fabia* and *M. lefroyi* from Ahmad and Gullamullah (1939) and those of *S. gregaria* from Hussain and Ahmad (1936). Therefore the agreement between theory and observation is all the more significant as there can be no question of the former influencing the latter. Of course where more than one humidity were tried we have taken the average for different humidities.



TABLE IV.

Comparison of Calculated and Observed Values of Developmental Periods.

Temp.	DEVELOPMENTAL PERIODS (IN DAYS).	
	Calculated.	Observed.
1. <i>Earias fabia</i> —Egg-Period.		
$y = 37.783e^{-0.001119(97.3-t^{\circ}\text{F})^2}$		
60.8°F.	11.78	11.58
68.0°F.	6.92	7.10
77.0°F.	4.19	4.16
86.0°F.	3.05	3.01
95.0°F.	2.66	2.68
2. <i>E. fabia</i> —Larval-Period.		
$y = 11.1e^{-0.001366(92.2-t^{\circ}\text{F})^2}$		
60.8°F.	34.64	34.96
68.0°F.	20.03	19.86
77.0°F.	12.02	11.92
86.0°F.	9.49	9.93
95.0°F.	9.12	8.90
3. <i>E. fabia</i> —Pupal-Period.		
$y = 13.69e^{-0.001107(97.3-t^{\circ}\text{F})^2}$		
60.8°F.	31.92	32.30
68.0°F.	18.89	18.32
77.0°F.	11.53	11.78
86.0°F.	8.41	8.39
95.0°F.	7.75	7.73
4. <i>E. fabia</i> —Life-cycle.		
$y = 4.51e^{-0.0013(93.3-t^{\circ}\text{F})^2}$		
60.8°F.	88.00	88.75
68.0°F.	51.20	50.68
77.0°F.	31.44	31.06
86.0°F.	23.83	24.43
95.0°F.	22.30	22.10
5. <i>M. lefroyi</i> —Egg-Period.		
$y = 183.7e^{-0.000872(103.5-t^{\circ}\text{F})^2}$		
60.8°F.	2.68	2.68
68.0°F.	1.64	1.63
77.0°F.	1.06	1.01
86.0°F.	0.71	0.71
95.0°F.	0.58	0.58
6. <i>M. lefroyi</i> —Larval-Period.		
$y = 54.1e^{-0.0011007(95.02-t^{\circ}\text{F})^2}$		
60.8°F.	6.70	6.40
68.0°F.	4.12	4.52
77.0°F.	2.64	2.56
86.0°F.	2.02	1.94
95.0°F.	1.85	1.89
7. <i>M. lefroyi</i> —Pupal-Period.		
$y = 20.66e^{-0.00112(96.6-t^{\circ}\text{F})^2}$		
60.8°F.	19.66	19.44
68.0°F.	12.10	13.01
77.0°F.	7.44	7.25
86.0°F.	5.48	5.23
95.0°F.	4.85	4.93
8. <i>S. gregaria</i> —Egg-Period.		
$y = 9.34e^{-0.002397(43-t^{\circ}\text{C})^2}$		
27.0°C.	19.77	20.00
30.0°C.	16.06	16.00
36.0°C.	12.05	12.00
40.0°C.	10.94	11.00
9. <i>S. gregaria</i> —Nymphal-Period.		
$y = 4.783e^{-0.005747(38.1-t^{\circ}\text{C})^2}$		
24.0°C.	64.01	63.00
25.0°C.	56.21	56.00
27.0°C.	42.54	46.50
30.0°C.	30.53	30.90
33.0°C.	24.34	25.50
36.0°C.	21.50	21.20
37.0°C.	21.10	20.90
40.0°C.	21.39	20.70
44.0°C.	25.60	27.00
10. <i>S. gregaria</i> —Life-cycle.		
$y = 1.0799e^{-0.004045(40.5-t^{\circ}\text{C})^2}$		
27.0°C.	97.00	97.40
30.0°C.	72.30	71.10
36.0°C.	50.20	50.80
40.0°C.	46.30	46.00

## IV. BIOPHYSICAL PROCESSES INVOLVED IN DEVELOPMENT.

The processes involved in organic development should be clear from the presumptions on which Equation I is based and the fact that the values based on this equation are in excellent agreement with values observed by various previous workers renders it highly probable that the presumptions are, if not quite correct interpretations of natural phenomenon, at least good guides for solving this complicated phenomenon. It will be noted that the following three fundamental hypotheses were made in deducing Equation I:—

- (1) Organic development takes place in accordance with the law of compound interest, the speed of vital activity acting as rate of interest.
- (2) The amount of development from birth to natural death as well as the amount of development required to complete the well-defined stages like egg, larva, pupa, etc., are constant quantities for the species, making of course allowance for individual variations.
- (3) The amount of vital activity performed in unit time increases with the rise of temperature but with a velocity which does not remain constant but remains continuously getting retarded with the same rise of temperature. The rate of retardation, however, has been supposed to be uniform.<sup>13</sup>

As regards the first presumption there is nothing new because a number of previous equations, e.g. principle of  $Q_{10}$  of van't Hoff,  $\mu$  of Arrhenius, the equation of catenary curve of Janisch, etc. are all based on the same hypothesis although that hypothesis itself was probably based only on an analogy of autocatalytic chemical reaction. The illustration of a developing embryo given in Section II, however, shows that there is no need of getting an analogy from the chemical field. Development does actually take place in geometrical progression, i.e., in accordance with compound interest law at least in earlier stages. Blackman (1919) discussed this fact at length so far as plant growth is concerned. As regards later stages of development although the geometrical progression gets masked due to differentiation of cells which gradually lose their meristematic properties, yet it is quite plausible to assume that the essential nature of development is not altered. Development may not and actually does not consist of only cell division but it is easily imaginable that it consists of activities analogous to the development and division of cells and the applicability of Equation I to observed facts concerning advanced stages of development gives experimental support to this assumption.

As regards second assumption also, there is nothing new. Even the simplest of the relations, namely, the straight line relationship between temperature and developmental indices, presumes the total development to be a constant quantity. Moreover the use of a quantity like developmental index as average velocity of development presupposes the total development to be constant. Anyway there appears to be no difference of opinion about this point.

The third presumption, however, is entirely new and it is this point which renders Equation I absolutely different from all other previous equations so far used to represent the relationship under consideration. It should be noted that this presumption is actually of composite nature and consists of two basic factors. According to this hypothesis the speed of vital activity, or let us say for convenience of terminology, the amount of vital activity performed in unit time increases with, say, a particular velocity due to rise of temperature and that velocity itself remains getting continuously retarded with the same rise of temperature. Now the same rise of temperature cannot be expected to create a positive velocity and a negative acceleration, i.e., retardation unless and until two opposite processes are involved and both

<sup>13</sup> To be more accurate it may be, however, mentioned here that the total weight of evidence is likely to indicate later on that retardation also is not uniform but goes on slowly increasing. This point will be fully analysed in a subsequent contribution.

of them are accelerated due to rise of temperature but their effects being opposite, one process acts as retardation for the other. Therefore if this third presumption is correct, as it is found to be, then it can be explained only in one way, namely, that the amount of vital activities ( $r$ ) performed in unit time increases due to rise of temperature with a particular velocity ( $u$ ), but simultaneously there is a sort of resistance against vital activities and this resistance also goes on increasing itself and consequently goes on retarding the velocity with which ( $r$ ) increases. Thus due to this additional and opposite process of resistance the change in the value of ( $r$ ) takes place like a retarded motion.

To sum up all the processes, the average velocity of development, i.e., value of developmental index, i.e., reciprocal of developmental period ( $y$  or  $1/P$ ) depends on the value of ( $g$ ) which is absolute velocity of development at any moment; then ( $g$ ) itself depends on the value of ( $r$ ), i.e., the velocity of vital activity; and ultimately as shown by Equation 4 the value of ( $y$ ) directly depends on the value of ( $r$ ) which itself at any particular temperature depends on the value of ( $u$ ) which is the velocity of change in ( $r$ ) due to one degree rise of temperature; further an additional factor of resistance to vital activities comes into play creating retardation ( $a$ ) in the value of ( $u$ ) and therefore the resultant velocity ( $v$ ) of change in ( $r$ ) at any particular temperature depends on the value of ( $a$ ). Thus ultimately the value of ( $y$  or  $1/P$ ) of a particular species at any particular temperature depends on the values of ( $u$ ) and ( $a$ ). Thus if ( $g$ ) is taken to represent the velocity of development, then ( $r$ ) represents the acceleration of ( $g$ ), ( $u$ ) represents acceleration of ( $r$ ), i.e., acceleration of acceleration, and ( $a$ ) represents the negative acceleration (retardation) of acceleration of acceleration of the velocity of development. The first acceleration, namely, ( $r$ ) acts like the rate of compound interest, i.e., it increases the value of ( $g$ ) as the rate of interest increases the value of capital put on compound interest; subsequent accelerations work in the usual way as acceleration works in the case of moving bodies.

It is instructive to appreciate that the combination of two different principles from the physico-chemical realms is not unexpected in the complex phenomenon of temperature effect on rate of organic development and growth. Organic development consists firstly of vital activities and secondly of accumulation of the products of those activities (e.g. addition of cells, etc.). Now the phenomenon of accumulation of the products takes place as expected in accordance with the law of compound interest, the first acceleration ( $r$ ) acting as the rate of interest—a phenomenon which has its analogue in autocatalytic chemical reaction. That this does and should do so is evident from every day's experience. The product of vital activities does not remain passive but itself begins to show activity similar to those as a result of which it has been produced. Thus a cell produced as a result of vital activities of previous cells does not remain passive but it also produces further cells. This is the same thing as an offspring not remaining passive but producing its own offspring. Further this is similar to the interest of a capital bearing its own interest, i.e., the principle of compound interest law.

Coming to the vital activities, an activity is always a result of force. Therefore, so far as the increase or decrease in the speed of activity is concerned, it is but natural that it should take place in accordance with the usual principles governing force and motion. Temperature in the case of vital reactions is equivalent to the impressed force in the case of moving bodies. A particular temperature is equivalent to a particular impressed force which should cause a particular acceleration because according to the established principles of force and motion a definite force produces a fixed acceleration other conditions remaining unaltered, as

$$\begin{aligned} \text{Force} &= \text{rate of change of momentum,} \\ &= \text{'' '' '' mass} \times \text{velocity,} \\ &= \text{mass} \times \text{rate of change of velocity (mass being invariable),} \\ &= \text{mass} \times \text{acceleration.} \end{aligned}$$

(NOTE.—This has been simply copied from a physics book.)

Also we find experimentally that corresponding to a fixed constant temperature there is a fixed value of ( $y$ ), hence a fixed value of ( $g$ ) and ultimately a fixed value of ( $r$ ), i.e., a particular temperature produces a particular value of ( $r$ ) which represents acceleration of developmental velocity. But as the temperature is raised it is equivalent to the increasing of the amount of impressed force which must change the value of acceleration. Thus each degree rise in temperature means increasing the force by a fixed unit which in turn must increase the value of acceleration by a fixed unit which we have represented by ( $u$ ). Further raising the temperature degree by degree means increasing the impressed force unit by unit which should have meant accelerating the acceleration unit by unit, i.e., uniformly, but an additional factor of resistance to vital activities comes into play which actually goes on retarding the secondary acceleration ( $u$ ). Thus the effect of temperature on the rate of organic development may be summed up by saying that the speed of vital activities is increased with temperature as distance is increased with time in the case of retarded motion, and this speed of vital activity increases the speed of development as rate of true compound interest increases the capital. I am not aware of any other phenomenon in nature in which these two different principles are combined as described above. There is no dearth of examples, however, wherein these principles are separately followed. Autocatalytic chemical reaction has already been cited as following the principle of compound interest. The principle of retarded motion is best illustrated by a bullet shot upwards when the bullet continues to go upwards till the retardation due to gravitational attraction does not become equal to the forward velocity of the bullet, then pauses a moment and then comes down.

Having understood all the biophysical processes and the mathematical relationship between them, it is worthwhile to summarise again how temperature affects development. As  $v = u - at$  (Eq. 5), it is clear that the value of ( $v$ ) goes on decreasing as ( $t$ ), i.e., temperature is increased but still, so long as ( $u$ ) is greater than ( $a \cdot t$ ), the value of ( $v$ ) remains positive, i.e., the value of ( $r$ ) and hence the value of ( $g$ ) and ( $y$ ) remain increasing, but when the temperature increases to such a value that  $u = a \cdot t$ , then the value of ( $v$ ) becomes zero, i.e., there is no change in the value of ( $r$ ) and hence in the value of ( $g$ ) and ( $y$ ); further when the value of ( $t$ ) rises still higher then ( $u$ ) becomes less than ( $a \cdot t$ ) and the value of ( $v$ ) becomes minus, i.e., the value of ( $r$ ) and hence the value of ( $g$ ) and ( $y$ ) begin to decrease with any further rise of temperature. Thus the value of developmental index should go on rising, i.e., the developmental period should go on decreasing up to a temperature when  $u = a \cdot t$ , i.e., when  $t = u/a = T$  and thence onwards the effect of temperature should be opposite, i.e., the development should be quickest when  $t = T$ . This is exactly what we find experimentally.

Thus the assumptions given in this paper not only provide easy and accurate methods for calculating values of developmental periods corresponding to any constant temperature or any range of fluctuating temperature (*vide* Pradhan, 1945 and 1946) but what is most important they give an insight into the possible processes involved in organic development and for the first time give a clear-cut explanation as to why the rise of temperature up to a certain degree accelerates development but beyond that value begins to have retardative effect.

## V. COMPARISON WITH PREVIOUS VIEWS.

For full information concerning the comparative merits of the various attempts made to establish relationship between temperature and organic development, reference may be made to the works of Bodenheimer (1926 and 1938), Zwolfer (1934), Shelford (1929), Wigglesworth (1942), Thompson (1942), and of Janisch (1932) who has made (in a number of papers from 1925 onwards) the latest fundamental

contribution on the subject. A number of botanists have also tried to solve the problem as will be seen from the works of Leitch (1916) and Barten-Wright (1933).

So far as the basic soundness and exactitude of agreement with observed data are concerned, Janisch (1932) has made a systematic comparison of the equation of his own catenary curve with the different equations put forward previous to him, and therefore it is needless to repeat the same comparison in this paper. Here it should suffice only to point out in what ways the present Equation I and the conceptions connected therewith show a definite advance over the knowledge accumulated up to the contribution of Janisch. He writes 'many efforts have been made to express these relations as a mathematical formula. They are separable into two groups. The first of them is based on velocity of reaction to chemical processes and represents an exponential function of various types (van't Hoff's rule, Arrhenius' formula, the exponential law of Janisch). In the other group the product of temperature and time expresses a constant. The formula taken as this relation is a hyperbola (thermal summation, Belehradek's formula, Wardle's formula and others). Naturally a formula must have a theoretical basis and must agree with the data observed. It is then certain that an exponential formula gives the best theoretical basis, since the chemical reactions as well as the biological phenomena at least depend upon the law of mass action from which the exponential formula (and therefore the exponential law also) follows automatically . . . . . However, the simple exponential curve does not agree with all observed data or with the biological situation. But the resultant of two crossing exponential curves described as catenary curve is smoothed to the observed points and agrees without exception with the biological situation.'

As quoted above, Janisch has rightly formed two basic criteria for selecting a valid formula. They are:

- (a) Sound theoretical basis,
- (b) Satisfactory agreement with observed data.

Judged from these criteria the second group of attempts putting forward non-exponential equations are naturally disposed of as unsatisfactory because neither they have any theoretical basis nor do they give good agreement with the observed facts. Out of the exponential equations which are supposed to have their theoretical basis in the law of mass action, Janisch has selected (on the basis of criterion b) what he calls catenary curve and which are actually two in number:

- (1) Symmetrical Catenary Curve

$$t = \frac{m}{2} (a^T + a^{-T})$$

- (2) Asymmetrical Catenary Curve

$$t = \frac{m}{2} (a_1^T + a_2^{-T})$$

wherein  $t$  = time,  $m$  = observed shortest time of development,  $a$  = constant and  $T$  = temperature.

Janisch also calls these curves 'Complex exponential as opposed to simple one which has the formula  $t = m \cdot a^T$ ', and on which other exponential curves put forward before Janisch were based and which did not prove to be satisfactory judged on the basis of criterion b. Now it is to be noted that Janisch has modified the equation of simple exponential curve into that of his own catenary curve only to satisfy the criterion b, i.e., in order to get satisfactory agreement with observed data, but by introducing the modification without fairly sound theoretical basis he has again made his own curve unsatisfactory from the view-point of criterion a. Coming to Equation I put forward in the present paper it will be found that although this

equation also happens to be a modification of simple exponential equation, the modifications are based on more definite theoretical considerations (as fully explained in Sections II and IV) which render our conception of whole developmental phenomenon far clearer than what it was so far. Further the present equation does not share the defects of the catenary curve; for example, the values of such fundamental constants as the shortest period of development ( $m$ ) and the temperature corresponding to the same have to be experimentally determined for the catenary curve and this is a very difficult task. For example, Janisch (1932) has taken for his illustration  $m = 3.75$  days corresponding to  $29.6^{\circ}\text{C}$ . Now in order to find out the exact value  $29.6$  one is bound to perform experiments at very short intervals of temperature in the neighbourhood of  $29$  and  $30$  besides the usual experiments to reach this neighbourhood. The task is all the more tedious because  $m$  is the value of developmental period corresponding not only to the temperature of quickest development but corresponding to the optimum temperature which also takes into consideration least mortality, least variation, etc. On the other hand, in the case of the present equation the values of  $y_0$  and  $T$  which represent quickest development and corresponding temperature are not to be determined experimentally but are to be calculated on the basis of all available data taken together (as shown in Appendix A). Consequently there is bound to be much less experimental error in  $y_0$  of the present equation than in  $m$  of catenary curve. As regards taking the optimum temperature instead of temperature of quickest development as the origin even of catenary curve I think it is unnecessarily confusing two different issues, namely, the effect of temperature on the velocity of development and the effect of temperature on mortality, variation, etc. However, it is not the purpose of this paper to discuss this last point in detail.

As regards the agreement with observed data I have already tackled this point in Section III and have shown how excellently the present equation is applicable to the data collected by various previous workers.

Last but not the least, the practical advantages strongly advocated by Bodenheimer (1938) in favour of hyperbolic equation also need consideration in this connection. According to this author, 'the three distinct advantages of equilateral hyperbola are:

- (1) The extremely simple way of computation, an important fact considering the mathematicophobia of most biologists.
- (2) The easy way of getting the basic data for calculation and of improving the curve by additional data.
- (3) Last but not the least, only hyperbola furnishes us with the value for lower developmental threshold which value has proven to be of highest importance in ecological conception and calculations. This value is not obtained by any other formula.'

Due to the virtues enumerated by Bodenheimer, hyperbolic equation is certainly today the most well known and hence *apparently* also the most exact relation between temperature and insect development. It is therefore necessary to emphasise:

- (a) that due to exact similarity between Equation I and the equation of normal frequency distribution, for which most of the necessary calculations have already been done and published for ready reference, the calculations with Equation I are in fact very simple and as shown in the previous communication (Pradhan, 1945) can easily be handled after a little practice even without thoroughly understanding the biological processes on which this equation is based;
- (b) that exactly the same basic data are needed for Equation I of this paper as for hyperbolic equation, i.e., a number of observations on developmental periods corresponding to different temperatures;

- (c) that it will be found from what has been given in a separate communication on biograph and biometer (Pradhan, 1946), that almost all the useful applications of the hyperbolic equation mentioned by Bodenheimer are possible with greater exactitude with the help of Equation I and without taking the help of threshold of development which has no scientific theoretical basis;
- (d) that besides retaining the three distinct advantages of hyperbolic equation, the present Equation I has rendered it possible (Pradhan, 1945) to evolve an equation for calculating developmental periods corresponding to variable temperatures of nature whereas all the previous equations are applicable, if at all, only to constant temperatures artificially maintained in the laboratory.

Long after writing the foregoing account I received some reprints kindly sent to me by Prof. Davidson of Waite Agricultural Research Institute, University of Adelaide, Australia, and another reprint kindly sent by Dr. C. B. Huffaker of Delaware, America. The work of Huffaker (1944) does not warrant any urgent discussion in this contribution but that of Davidson (1942 and 1943) necessitates the following remarks. Prof. Davidson has tried to fit to the temperature-development data on insect eggs the famous Verhulst-Pearl logistic curve which he, like many others, had previously used 'to describe the trend of growth in animal populations'. This is certainly a step in the expected though not altogether right direction. In fact it was surprising that the so well talked about logistic curve did not attract the attention when so many far less likely empirical formulæ have been tried by students of temperature-development relation. The logistic curve, in all its essentials, has been arrived at independently by chemists, biologists and mathematicians and all of them have found it useful and full of meaning and it is but natural that Prof. Davidson being interested both in the growth of animal population for which this curve was primarily developed as well as in the temperature-development relation should be impressed by the similarity between the so-called sigmoid curves of both these phenomena. But, it may be pointed out that as explained by Thompson (1942) the logistic curve is an integration or summation curve the differential of which 'is closely akin to the Gaussian curve of error and that the logistic curve describes the actual growth of an individual or a population and not the rate of growth. Further, if the logistic curve describes the actual growth, the rate of growth should naturally be described by a curve akin to the differential of logistic curve, and what we deal with in our study of temperature-development relation is rate of growth and development and not the actual growth and development.<sup>14</sup> Therefore Equation I of this paper, which is mathematically identical (although based on different hypotheses) with the Gaussian curve of error, is a natural outcome of the applicability of the logistic curve to the growth of an individual or a population. Davidson's attempt, on the other hand, to fit the same logistic curve to the actual growth (of population) and to the rate of growth or development is defective in principle, howsoever close a fit might be obtained within a particular range. This defect in principle also exhibits itself in practice as the logistic curve becomes asymptotic

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<sup>14</sup> In this connection it must be pointed out that the logistic curve has been applied to the actual growth of an individual or a population plotted against time. Therefore the differential of the logistic curve which has been recognised to be akin to the normal curve is ordinarily the curve obtained by plotting the rate of growth against time, i.e., the age of the individual or population. In the case of temperature-development curve, on the other hand, the rate of development is plotted against temperature and not against time. Therefore the fact that the same type of curve is obtained when the rate of development is plotted either against time or against temperature, is very instructive, indicating that probably time and temperature are similar in their action on rate of development.

to the top horizontal line and generally does not come down, whereas the temperature-development curve invariably comes down after the peak temperature. Davidson has tried to overcome this criticism by doubting the existence of a smooth downward curve beyond the peak temperature and by saying that because of the harmful effects of higher temperatures the observed data for temperatures above the peak will be less reliable than data for temperatures below the peak. This reasoning is certainly very weak. The descending of the curve beyond the peak is too universal to be ignored or doubted. All the figures given by Davidson himself (1942) and by Davidson and Swan (1943) give unmistakable evidence of this descending portion of the curve. Thompson (1942) in his instructive review states, 'We see that there are always certain temperatures at which the rate is maximum; while on either side of the optimum the rate falls off after the fashion of a normal curve of error.' In this statement we also see that Thompson did recognise the similarity between temperature-development curve and the normal curve but he did not pursue the subject further.

In the end it may also be pointed out that the logistic curve as applied by Davidson also possesses the defect pointed out in the case of catenary curve, namely, that 'the peak temperature must be carefully determined by experiment' and what this operation practically means has already been explained in the case of catenary curve.

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#### VII. SUMMARY.

This contribution embodies certain findings regarding the effect of temperature on the rate of organic development. These findings are certainly of immense practical utility and they are likely to prove of much theoretical interest.

From practical point of view the paper presents an elaboration of proof in favour of a method reported in an earlier communication of estimating the duration of life cycles and developmental periods of insect stages under any constant temperature or any range of temperature fluctuation. From the theoretical point of view it puts forward a far clearer conception than what has been held or reported so far, of the phenomenon of temperature effect on the rate of organic development. *For the first time a clear-cut explanation is being given as to why the rise of temperature up to a certain degree accelerates development but beyond that value begins to have retardative effect.* The three main hypotheses formulated in this connection are the following:—

- (1) Organic development takes place in accordance with the law of *compound interest*, the speed of vital activities acting as rate of interest.
- (2) The amount of development from birth to death and the amount of development required to complete the well-defined stages like egg, larva, pupa, etc. are constant quantities for the species, making of course allowance for individual variations.
- (3) The amount of vital activity performed in unit time increases with the rise of temperature but with a velocity which does not remain constant and remains continuously getting retarded with the same rise of temperature. The rate of retardation, however, has been supposed to be uniform.

The ideas contained in the first two presumptions do partly exist in literature, but the third presumption is entirely new. The equation based on these hypotheses have been found to fit satisfactorily to ten different sets of observations of previous workers so far examined on developmental periods of various stages of three species of insects belonging to three different orders.



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## APPENDIX A.

For fitting equation  $Y = AX^2 + BX + C$  to the observations on pupal periods of *E. fabia* under different constant temperatures we proceed as follows:

First we prepare the following table in which

$P$  = Developmental periods calculated from the data published by Ahmad and Gulamullah (1939) after taking the average of their averages of pupal periods corresponding to three humidities for each value of temperature.

$X$  = Values of temperature in degrees Fahrenheit corresponding to different values of  $P$ .

$$Y = \text{Log } y, \text{ where } y = \frac{100}{P}.$$

X	X <sup>2</sup>	X <sup>3</sup>	X <sup>4</sup>	P in days.	Y	XY	X <sup>2</sup> Y
60.8	3696.64	224755.712	13665147.2896	32.31	0.49068	29.833344	1813.8673
68	4624.00	314432.000	21381376.0000	18.32	0.73704	50.118720	3408.0730
77	5929.00	456533.000	35153041.0000	11.78	0.92886	71.522220	5507.2109
86	7396.00	636056.000	54700816.0000	8.39	1.07631	92.562660	7960.3888
95	9025.00	857375.000	81450625.0000	7.33	1.13483	107.808850	10242.8407
386.8	30670.64	2489151.712	206351005.2896		4.36772	351.845794	28931.3807
$\Sigma(X)$	$\Sigma(X^2)$	$\Sigma(X^3)$	$\Sigma(X^4)$		$\Sigma(Y)$	$\Sigma(XY)$	$\Sigma(X^2Y)$

Substituting the values obtained above in a set of normal equations we get

- (a)  $A\Sigma(X^4)+B\Sigma(X^3)+C\Sigma(X^2) = \Sigma(X^2Y)$  or  $206351005\cdot2896A + 2489151\cdot712B + 30670\cdot64C = 28931\cdot3807$ .
- (b)  $A\Sigma(X^3)+B\Sigma(X^2)+C\Sigma(X) = \Sigma(XY)$  or  $2489151\cdot7120A + 30670\cdot640B + 386\cdot80C = 351\cdot8460$ .
- (c)  $A\Sigma(X^2)+B\Sigma(X)+NC = \Sigma(Y)$  or  $30670\cdot6400A + 386\cdot800B + 5\cdot00C = 4\cdot36772$ .
- (d)  $12445758\cdot560A + 153353\cdot2B + 1934\cdot0C = 1759\cdot22897$  (multiplying (b) by 5).
- (e)  $11863403\cdot552A + 149614\cdot24B + 1934\cdot0C = 1689\cdot434096$  .. .. [(c)  $\times$  386.8].
- (f)  $582355\cdot008A + 3738\cdot96B + 0 = 69\cdot794874$  .. .. [(d)-(e)].
- (g)  $1031755026\cdot4480A + 12445758\cdot560B + 153353\cdot2C = 144656\cdot903626$  .. .. [(a)  $\times$  5].
- (h)  $940688158\cdot0096A + 11863403\cdot552B + 153353\cdot2C = 133959\cdot767741$  .. .. [(c)  $\times$  30670.64].
- (i)  $91066868\cdot4384A + 582355\cdot008B + 0 = 10696\cdot135885$  .. .. [(g)-(h)].
- (j)  $339137355342\cdot68A + 2177402080\cdot711B = 40645394\cdot406629$  .. .. [(f)  $\times$  582355.008].
- (k)  $340495378416\cdot44A + 2177402080\cdot711B = 39992424\cdot229327$  .. .. [(i)  $\times$  3738.96].
- (l)  $-1358023073\cdot76A + 0 = 652970\cdot177302$  .. .. [(j)-(k)].

$A = -0.0004808241$ .

Substituting the value of A in (f) we have  $B = +0.09355682$ .

Substituting the values of A and B in (c) we have  $C = -3.414575$ .

$T = \frac{B}{2A} = \frac{0.09355682}{2 \times -0.0004808241} = 97.3$  or  $T = 97.3$ .

$\log y_0 = \log K = C - AT^2 = 1.1364$  or  $y_0 = 13.69$ .

$-\frac{1}{2a} = \frac{A}{.4343}$  or  $\frac{1}{2}a = -0.001107$ .

The equation thus comes to be:  $y = 13.69e^{-0.001107(97.3-t^2)^2}$ .

APPENDIX B.

The following Doolittle procedure for fitting equation  $Y = AX^2+BX+C$  to the raw individual observations on developmental periods under different constant temperatures was adapted from the book of Goulden (1939).

The following table was prepared from the observations on nymphal periods of *S. gregaria* published by Hussain and Ahmad (1936) in their Tables XIX and XXI. In the following table  $P$  = nymphal period in days,  $t$  = temperature in degrees centigrade and numbers within the table represent the number of nymphs

TABLE B<sub>1</sub>.

P ↓	t→	24°C.	25°C.	27°C.	30°C.	33°C.	36°C.	37°C.	40°C.	44°C.	N <sub>yx</sub>
19 days								1	2		3
20 "							3	2			5
21 "							10	3	12		25
22 "						1	7	1			9
23 "						1					1
24 "						2					2
26 "						8					8
27 "						5				1	6
30 "					2						2
31 "					13						13
45 "				1							1
46 "				2							2
47 "				4							4
56 "			1								1
62 "		3									3
63 "		1									1
64 "		2									2
N <sub>xy</sub> →		6	1	7	15	17	20	7	14	1	= 88

which reached the adult stage at each temperature. Thus the table shows that at 24°C. 3 nymphs reached the adult stage in 62 days, 1 in 63 days and 2 in 64 days, and the total number of successful observations ( $N_{xy}$ ) at 24°C. was 6.

From the above table ( $B_1$ ) we prepare the following one in which  $P$  is replaced by  $Y$  when  $Y = \log 100 - \log P$ , i.e., logarithm of developmental index;  $X = t$ .

TABLE  $B_2$ .

$Y \quad X \rightarrow$ ↓	24	25	27	30	33	36	37	40	44	$N_{yx}$
0.7212							1	2		3
0.6990						3	2			5
0.6772						10	3	12		25
0.6576					1	7	1			9
0.6383					1					1
0.6198					2					2
0.5850					8					8
0.5686					5					6
0.5229				2					1	2
0.5086				13						13
0.3468			1							1
0.3372			2							2
0.3279			4							4
0.2518		1								1
0.2076	3									3
0.2007	1									1
0.1938	2									2
$N_{xy} \rightarrow$	6	1	7	15	17	20	7	14	1	= 88

From Table  $B_2$  we construct Table  $B_3$  in which  $T_{yx}$  is calculated as given for column of  $X = 24$  as example:

$$\begin{aligned}
 0.2076 \times 3 &= 0.6228 \\
 0.2007 \times 1 &= 0.2007 \\
 0.1938 \times 2 &= 0.3876
 \end{aligned}$$

$$T_{yx} = 1.2111$$

Thus the value of  $T_{yx}$  against 24 of column  $X$  comes to be 1.2111; other columns are self-explanatory.

TABLE  $B_3$ .

$X$	$N_{xy}$	$T_{yx}$	$X \cdot N_{xy}$	$X^2 \cdot N_{xy}$	$X^3 \cdot N_{xy}$	$X^4 \cdot N_{xy}$	$X \cdot T_{yx}$	$X^2 \cdot T_{yx}$
24	6	1.2111	144	3456	82944	1990656	29.0664	679.5936
25	1	.2518	25	625	15625	390625	6.2950	157.3750
27	7	2.3328	189	5103	137781	3720087	62.9856	1700.6112
30	15	7.6576	450	13500	405000	12150000	229.7280	6891.8400
33	17	10.0585	561	18513	610929	20160657	331.9305	10953.7065
36	20	13.4722	720	25920	933120	33592320	484.9992	17459.9712
37	7	4.8084	259	9583	354571	13119127	177.9108	6582.6996
40	14	9.5688	560	22400	896000	35840000	382.7520	15310.0800
44	1	.5686	44	1936	85184	3748096	25.0184	1100.8096
	88	49.9298	2952	101036	3521154	124711568	1730.6859	60854.6867
( $N$ )	$\Sigma(Y)$	$\Sigma(X)$	$\Sigma(X^2)$	$\Sigma(X^3)$	$\Sigma(X^4)$	$\Sigma(X^4)$	$\Sigma(XY)$	$\Sigma(X^2 Y)$

From this table ( $B_3$ ) we continue the calculation in Table  $B_4$  according to the instructions given therein. In these instructions expression like (5, 1) means figures given in line 5 column 1 of  $B_4$ ; expression like (1) means all the figures given in different columns of line 1.

TABLE  $B_4$ .

Instructions.	Column 1 → Line ↓	0	1	2	K	Sum.
		(N)	$\Sigma(X)$	$\Sigma(X^2)$	$\Sigma(Y)$	
Insert N, $\Sigma(X)$ , $\Sigma(X^2)$ and $\Sigma(Y)$ ..	1	88-0000	2952-0000	101036-0000	49-9298	+ 104125-9298
(1) ÷ (1, 0) and change sign	2	-1-0000	-33-5454	-1148-1364	-0-5674	- 1183-2492
			$\Sigma(X^2)$	$\Sigma(X^3)$	$\Sigma(XY)$	
Insert $\Sigma(X^2)$ , $\Sigma(X^3)$ and $\Sigma(XY)$ ..	3		101036-0000	3521154-0000	1730-6859	+ 3623920-6859
(1) × (2, 1) ..	4		-99026-0208	-3389293-0344	-1674-9151	-3489993-9703
(3) + (4) ..	5		2009-9792	131860-9656	55-7708	+ 133926-7156
(5) ÷ (5, 1) and change sign	6		-1-0000	-65-6031	-0-02775	- 66-63085
				$\Sigma(X^4)$	$\Sigma(X^2 Y)$	
Insert $\Sigma(X^4)$ and $\Sigma(X^2 Y)$	7			124711568-0000	60854-6867	+ 124772422-6867
(1) × (2, 2) ..	8			-116003109-3104	-57326-2208	-116060435-5312
(5) × (6, 2) ..	9			-8650488-1123	-3658-7374	-8654146-8497
(7) + (8) + (9)	10			57970-5773	-130-2715	+ 57840-3058
(10) ÷ (10, 2) and change sign ..	11			-1-0000	+0-0022472	-0-9977528
$A = -0-002247$				$-0-002247(A) =$	$-0-002247(11,$ $K)$ with sign changed.	
$B = +0-17516$			$+0-17516(B) =$	$+0-14741 [(A)$ $\times (6, 2)]$	$+0-02775 (6,$ $K)$ with sign changed.	
$C = -2-7285$		$-2-7285 =$	$-5-8758 (B)(2, 1)$	$+2-5799 [(A)$ $\times (2, 2)]$	$+0-5674 (2, K)$ with sign changed.	
Check		-240-1344	+517-1107	-227-0481	= 49-9282	

$$\therefore Y = -0-0022472X^2 + 0-175173X - 2-7288.$$

Further calculations as in Appendix A.

Analysis of Variance Test for Goodness of Fit is given in the main body of paper in Table III.