

THE INFLUENCE OF TEMPERATURE ON THE RATE OF DEVELOPMENT OF INSECTS, WITH SPECIAL REFERENCE TO THE EGGS OF *GRYLLULUS COMMODUS* WALKER

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Summary

Eggs of the cricket *Gryllulus commodus* Walker† (Gryllidae, Orthoptera) were incubated at nine constant temperatures; the mean duration of the incubation period and its variance have been determined at each temperature.

The mean rate of development of the eggs, expressed as percentage development per day, has been plotted against temperature, and a logistic curve having the form

$$Y = \frac{14.0906}{1 + e^{5.848176 - 0.223386t}}$$

derived from the data by the method of maximal likelihood, is shown drawn through the observed points. The observed points can be seen to lie closely along the calculated curve, yet the departures of the observed means from the calculated values, though small, are highly significant.

Two other cases in which logistic equations had been used to express the trend in rate of development of insect eggs with change in temperature and which on visual inspection appear to be excellent fits, have been re-examined and in each the observed means depart significantly from the calculated values.

The departure of the observed means from the theoretical curve is shown to increase as the period of development is extended to include post-embryonic stages of development.

Two or more developmental stages differing in their response to change in temperature may not be considered together when attempting to express trend in rate of development by means of a logistic curve. Since all stages during embryogenesis are unlikely to respond in exactly the same way to change in temperature, it is concluded that the logistic curve cannot be used to express precisely the trend in the rate of development of eggs at different temperatures. Whether the trend of a stage of development responding uniformly in its rate of development to change in temperature conforms to a logistic curve remains an open question.

I. INTRODUCTION

Many attempts have been made from time to time to describe the quantitative relationship that exists between temperature and the rate of development of poikilothermic animals by means of mathematical equations. The

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† *Gryllulus commodus* Walker has long been known in the Australian literature as *G. servillei* Saussure. The former name has been adopted on the authority of Dr. L. Chopard of the Paris Museum, to whom specimens were submitted through the Commonwealth Institute of Entomology, London. See also Uvarov (1935).

earlier literature on this subject has been reviewed by Belerádek (1935), Needham (1942), and Fry (1947).

In 1942, Davidson proposed the use of the logistic curve, developed by Pearl and Reed (1920) for use in describing the growth of populations, to express the relationship between temperature and the rate of development of insects and in 1944 he elaborated this concept and gave an outline of a graphical method of deriving the constants in the logistic equation. He concluded that the logistic, when so derived, followed the observed trend in rate of development more closely and over a wider range of temperatures than any other curve in use up to that time. Also in 1944, Birch applied the method of maximal likelihood in estimating the parameters in the logistic equation and found what was apparently a statistically insignificant departure of the observed mean values from the expected values calculated from the logistic equation.

The present paper is concerned with an analysis of results obtained for the eggs of the Australian black field cricket, *Gryllulus commodus* Walker, and a re-examination of some earlier data in the light of this analysis.

II. EXPERIMENTAL MATERIAL AND METHODS

A large number of crickets were caught as late instar nymphs in the field at Blackwood, near Adelaide, and were kept in humid cages in a glass-house until they reached maturity. They were fed on grass and wheat grains. When most of the crickets had reached the adult stage, shallow trays of moist sand were introduced into the cages into which the females oviposited freely.

The trays were removed daily and the eggs sieved out under water. All the eggs laid on any one day were collected together, labelled, and placed in an incubator at 12.8°C., where they remained for 30-40 days. This cold temperature treatment was necessary since the eggs at the time of laying were either in a state of diapause or diapause supervened soon after, and it was known that with about 30 days treatment at 12.8°C., it was possible to obtain eggs uniformly free from diapause. During this period little or no morphological development occurred. Diapause will not be considered further here as it forms the subject of a later paper.

Experiments were done at nine constant temperatures (see Table 2 for the ranges of the thermostats). For each temperature treatment five batches of 50 eggs each were used, each batch being placed on moist blotting paper in a petri dish. The petri dishes were placed on stands in air-tight glass jars in the bottom of which was 100 ml. of distilled water, since previous experience had shown that unless the relative humidity in the jars was close to 100 per cent. most of the eggs died.

The number of nymphs that had hatched was recorded every 24 hours at temperatures up to and including 23.3°C. From 25.8 to 28.7°C. inclusive counts were made every 12 hours and at 31.5 and 33.8°C. every 8 hours. The shorter intervals were necessary at the higher temperatures to equalize, as far as possible, the loss of information for each temperature treatment.

Temperature readings were taken at 9 a.m. each morning and the mean value assessed from these.

Since it was not possible to do all nine temperature treatments concurrently a control experiment was done at 26.8°C. with each group of treatments. Thus the temperature treatments 16.4, 19.4, 21.1, 23.3, and 26.8°C. (control I) were done together, treatments 25.8, 28.7, and 26.8°C. (control II) together, and treatments 31.5, 33.8, and 26.8°C. (control III) together. The second control lot, II, contained only three batches or 150 eggs, but since it was observed for hatchings every 12 hours, whereas I and III were observed only every 24 hours, it was used to estimate the duration of the incubation period at this temperature.

TABLE I
MEAN DURATION OF THE INCUBATION PERIODS OF THREE LOTS OF EGGS
USED AS CONTROLS

Control No.	Mean Duration of Incubation Period (hr.)			
I	309.6			
II	314.9			
III	314.3			
ANALYSIS OF VARIANCE OF CONTROL LOTS				
Source of Variation	Degrees of Freedom	S.S.	M.S.	V.R.
Between lots	2	3502	1751	7.66*
Error	584	133549	228.7	
Total	586	137051		

* Significant at $P = 0.001$.

Analysis of the differences in the mean duration of the incubation period in the three control lots of eggs is shown in Table 1. The difference in the mean of I from those of II and III, though small, is highly significant. This difference may be due to either or both of two causes; the eggs in II and III may have been different from those in I in developing more slowly, or the environment in which they developed may have been different. Control I was incubated in a different thermostat from II and III because at the time the latter were started this was needed for other work. Examination of the daily temperature records of the two thermostats used suggests that the mean temperature for the whole period was about 0.1°C. higher for I than for the other two. This is due to the difficulty involved in setting two thermostats to the same temperature. Examination of Figure 1 shows that a difference of this order would be sufficient to account for the difference in the mean duration of the incubation periods.

The analysis of variance presented in Table 1 shows that the precision obtained in estimating the residual variance has made it possible to demonstrate the significance of as small a difference as about one-quarter of the group interval used in estimating the means.

From these considerations, those treatments for which lot I was the control, namely 16.4, 19.4, 21.1, and 23.3°C., were included in the observations as "normal" eggs.

III. RESULTS

Table 2 sets out the mean duration of the incubation period and the mean percentage development per day for eggs at each of the nine constant temperatures. The ranges of the thermostats are given in parentheses in column 2.

TABLE 2
OBSERVED MEAN DURATION OF THE INCUBATION PERIOD AND PERCENTAGE DEVELOPMENT PER DAY AT SEVEN CONSTANT TEMPERATURES

Array No.	Temperature (°C.)	Mean Duration of Incubation Period (days)	Mean Percentage Development per Day (\bar{y}_i)
1	19.4 (± 0.4)	39.59	2.5295
2	21.1 (± 0.5)	29.34	3.4121
3	23.3 (± 0.1)	20.26	4.9433
4	25.8 (± 0.1)	14.95	6.6979
5	26.8 (± 0.1)	13.12	7.6377
6	28.7 (± 0.2)	11.25	8.9107
7	31.5 (± 0.1)	9.28	10.7989

The mean percentage development per day at any temperature is estimated according to the equation

$$\bar{y}_i = \frac{\sum f 100/d}{n},$$

where

\bar{y}_i = the mean percentage development per day,

f = the numbers of eggs that had hatched at each observation,

d = the duration of the incubation period at each observation, and

n = the total number of eggs hatching at the particular temperature.

Davidson (1944), following a graphical method of determining the constants in his equations as given by Pearl (1930), showed that when percentage development per day is plotted against temperature the resulting points appear to lie very closely along a logistic curve whose equation is

$$Y = \frac{K}{1 + e^{a + bt}},$$

where

Y = percentage development per day,

K = the parameter representing the interval between the upper and lower asymptotes of the curve,

a = the parameter determining the relative position of the origin of the curve on the abscissa,

b = the parameter determining the slope and course of the curve, and

t = temperature (°C.).

Subsequently Birch (1944) employed the method of maximal likelihood to determine the constants of the best-fitting logistic curve and the same procedure has been used here, giving the equation

$$Y = \frac{14.0906}{1 + e^{5.848176 - 0.223386t}}$$

for the data in Table 2. This curve is shown in Figure 1 plotted through the observed points.

The observed values of percentage development per day for the temperature arrays at 16.4 and 33.8°C. have been omitted in the calculation of the

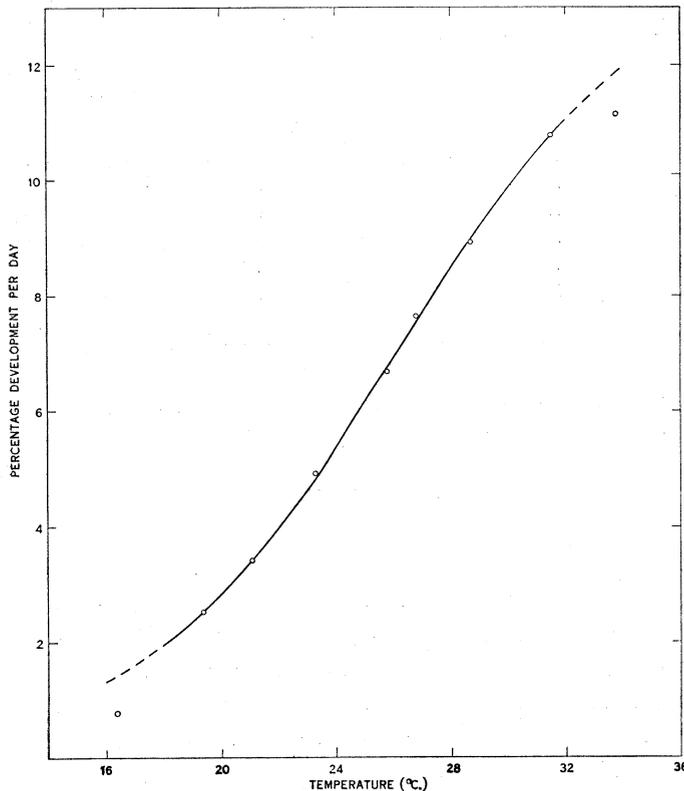


Fig. 1.—Logistic curve of form $Y = \frac{14.0906}{1 + e^{5.848176 - 0.223386t}}$ for the development of the eggs of *Gryllulus* drawn through the observed means.

curve since it is clear from Figure 1 that at both these temperatures development was retarded below the expected rate.

Visual inspection of Figure 1 indicates that all the observed points for temperatures between 19.4 and 31.5°C. inclusive lie closely along the calculated curve, but it is necessary to apply an objective statistical test to assess the goodness of fit.

Table 3 sets out the calculations involved in testing the goodness of fit of the calculated logistic. In column 5 are shown the deviations of the observed means from expectation ($\bar{y}_i - Y_i$), whilst in column 6 the values of s_i^2 , the variance of the mean for each temperature array, are given. The figures in column 2 are the numbers of observations on which each mean is based.

χ^2 is estimated according to the equation

$$\chi^2 = \sum (\bar{y}_i - Y_i)^2 / s_i^2,$$

where

\bar{y}_i = the observed mean percentage development per day for any temperature array,

Y_i = the calculated value of percentage development per day for that array, and

s_i^2 = the estimated variance of the mean of the array.

χ^2 has 4 = (n - 3) degrees of freedom.

TABLE 3
GOODNESS OF FIT OF CALCULATED LOGISTIC CURVE FOR THE RATE OF DEVELOPMENT OF THE EGGS OF *GRYLLULUS COMMODUS*

Temp. (°C.)	n	\bar{y}_i	Y_i	$(\bar{y}_i - Y_i)$	s_i^2	χ^2
19.4	212	2.5295	2.5402	- 0.0107	0.000034	3.37
21.1	227	3.4121	3.4281	- 0.0160	0.000065	3.94
23.3	222	4.9433	4.8543	+ 0.0890	0.000162	48.90
25.8	232	6.6979	6.7468	- 0.0489	0.000294	8.13
26.8	142	7.6377	7.5327	+ 0.1050	0.000900	12.25
28.7	231	8.9107	8.9778	- 0.0671	0.000725	5.99
31.5	234	10.7989	10.8000	- 0.0011	0.001181	0.00
Total				- 0.0183		82.57

χ^2 at $P = 0.05$ with 4 degrees of freedom = 9.5.

The test must be performed in this manner since the intra-array variances differ significantly. It should be pointed out that the test is only approximate since the estimated array variances have been substituted for the unknown true variances, but in this particular case the use of the true χ^2 distribution will yield an accurate estimate of the probability since the array variances have been estimated with considerable precision.

When this test of goodness of fit was applied to the calculated curve, χ^2 was found to be significantly too large, 82.6 (Table 3, column 7), the value of χ^2 at $P = 0.05$ being 9.5.

A comparison between columns 5 and 6 in Table 3 shows that the differences between the observed and calculated values of percentage development per day are very large, relative to the standard deviations of their respective array means, at all temperatures except 31.5°C.; so large in fact that differences of this order over the seven arrays are unlikely to be attributable to chance.

This result was surprising in view of the fact that Birch (1944) in his work with *Calandra oryzae* found an insignificant value of χ^2 . Figure 2 shows

the logistic curve derived by the method of maximal likelihood for the eggs of *C. oryzae* at moisture level I drawn through the observed points; the figure is redrawn from the data in Birch (1944). Table 4 shows the correct details of the calculation of χ^2 for Birch's data. The value of χ^2 , 29.6, contrasts strongly with Birch's result of 0.1821, the discrepancy being due to the fact that Birch, in making his calculations, was following advice in which the intra-array variances were unfortunately substituted for the variances of the array means.

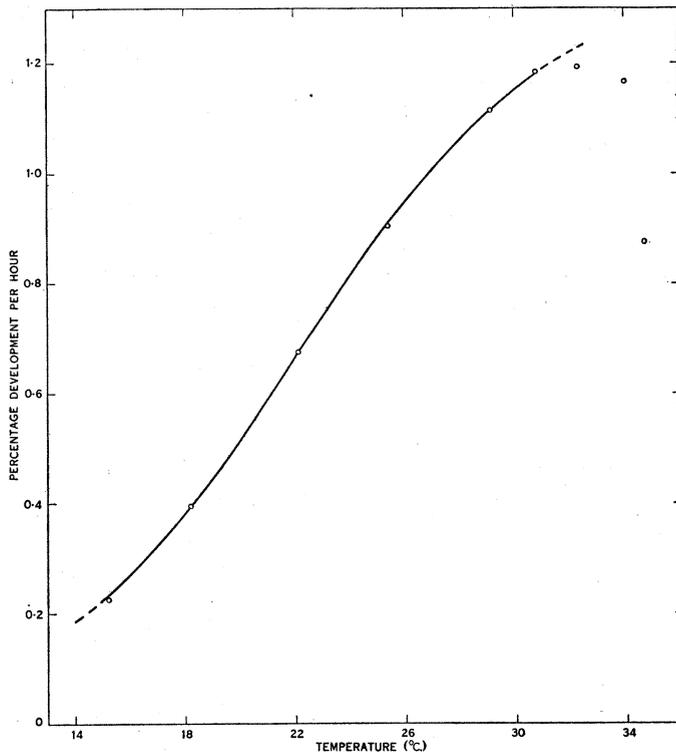


Fig. 2.—Logistic curve of form $Y = \frac{1.35062}{1 + e^{4.98145 - 0.2285t}}$ for the development of the eggs of *Calandra* drawn through the observed means (redrawn from Birch 1944).

It is evident that the observed values for percentage development per hour for these eggs also depart significantly from the calculated curve (at $P = 0.05$, $\chi^2 = 7.8$, with 3 degrees of freedom). Thus it is again found that the logistic curve is inadequate to express precisely the trend in rate of development of eggs with change in temperature, even though, in this case, elaborate precautions were taken to exclude as many variables as possible from the environment (cf. Birch 1944).

Further confirmation was sought by a re-examination of the data for *Drosophila melanogaster* given by Powsner (1935) and used by Davidson (1944) in proposing the use of the logistic curve. Figure 3 shows the logistic

derived by Davidson using the graphical method. It was not possible to use the iterative method of closer approximation on these data, as the only figures available were the mean durations of the incubation periods at the different constant temperatures and the standard deviations of these means. The frequencies and class intervals within each temperature array were, of course, not given in Powsner's paper.

In Table 5 are shown the values of \bar{y}_i for each temperature array, arrived at by dividing 100 by the value for the mean duration of the incubation period at each temperature. This introduces a small error (cf. the method given on p. 99) which is, however, probably not sufficiently large to influence the calculations to any appreciable extent. The values $s^2\bar{y}_i$ given in column 5 were calculated from the standard deviation of each mean as given by Powsner, from the equation

$$s^2\bar{y}_i = \frac{100^2 s^2x_i}{\bar{x}_i^4}$$

where

$s^2\bar{y}_i$ = the variance of the mean percentage development per hour, and

s^2x_i = the variance of the mean duration of the incubation period, as given.

TABLE 4

GOODNESS OF FIT OF CALCULATED LOGISTIC CURVE FOR THE RATE OF DEVELOPMENT OF THE EGGS OF *CALANDRA ORYZAE* AT MOISTURE LEVEL I (DATA FROM BIRCH 1944)

Temp. (°C.)	<i>n</i>	\bar{y}_i	Y_i	$(\bar{y}_i - Y_i)$	s_i^2	χ^2
15.2	140	0.226	0.233	-0.007	0.000002	22.4
18.2	215	0.395	0.394	+0.001	0.000003	0.4
22.1	197	0.677	0.671	+0.006	0.000007	5.1
25.4	186	0.905	0.911	-0.006	0.000023	1.5
29.1	175	1.114	1.114	-0.000	0.000044	0.0
30.8	192	1.184	1.181	+0.003	0.000061	0.1
Total				-0.003		29.6

χ^2 at $P = 0.05$ with 3 degrees of freedom = 7.8.

Column 7 of Table 5 shows that the discrepancies between the observed means, \bar{y}_i , and the calculated values, Y_i , when considered over all temperature arrays are again too great to be attributable to chance. Strictly the χ^2 test used here may only be applied after the method of maximal likelihood has been used to determine the adjustable parameters in the logistic equation but it should give a sufficiently approximate estimate of the goodness of fit for the purpose at hand.

IV. DISCUSSION

The application of the χ^2 test of goodness of fit to the three logistic curves presented in Figures 1, 2, and 3, shows that all three are inadequate representations of the observed trend in rate of development of eggs at different constant temperatures, despite the fact that on visual inspection the observed

points lie closely along the calculated curve. This is so even when the adjustable parameters of the curves have been derived by the method of maximal likelihood. Since this has been demonstrated for three independent sets of data, on the eggs of insects belonging to three widely separate orders, it can be expected to hold for all data of this kind obtained with corresponding precision.

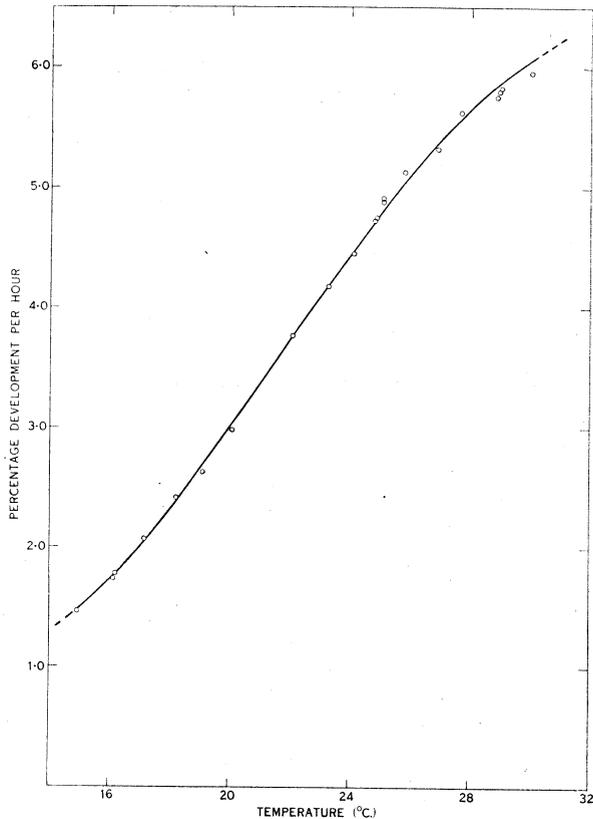


Fig. 3.—Logistic curve of form $Y = \frac{7.095}{1 + e^{4.4514215 - 0.2071879t}}$ for the development of the eggs of *Drosophila* drawn through the observed means (redrawn from Davidson 1944).

Two explanations of this state of affairs are open; either the data are too crude to fit the true logistic trend, or the logistic curve does not express the trend in rate of development with changing temperature, as it has been assessed in the experiments.

With regard to the first of these two possibilities, examination of the columns of variances of the means given in Tables 3, 4, and 5 shows that the means have been determined with precision, owing largely to the high numbers of replicates used in the experiments. However, it may be that the assessment of the actual temperatures at which the eggs developed was not sufficiently precise. The temperatures used in the calculations are estimates of

the temperatures within the glass jars or vials used as cages in the experiments and these containers, because of their bulk, are much less subject to temperature fluctuations than are the thermometers used. In the data for *Calandra* the temperature of each experiment was calculated as the arithmetic mean of a large number of readings and so will be a precise estimate of the actual temperature at which the eggs developed. Powsner would seem to have

TABLE 5

GOODNESS OF FIT OF CALCULATED LOGISTIC CURVE FOR THE RATE OF DEVELOPMENT OF THE EGGS OF *DROSOPHILA MELANOGASTER* (DATA FROM POWSNER 1935)

Temp. (°C.)	<i>n</i>	\bar{y}_i	Y_i	$(\bar{y}_i - Y_i)$	s_i^2	χ^2
14.95	54	1.4728	1.4561	+ 0.0167	5.1×10^{-5}	5.4
16.16	182	1.7361	1.7666	- 0.0305	1.3×10^{-5}	71.1
16.19	153	1.7762	1.7758	+ 0.0004	1.4×10^{-5}	0.0
17.15	129	2.0534	2.0535	- 0.0001	2.6×10^{-5}	0.0
18.20	64	2.4155	2.3849	+ 0.0306	8.7×10^{-5}	10.7
19.08	94	2.6309	2.6819	- 0.0510	1.7×10^{-5}	156.0
20.07	82	2.9904	3.0313	- 0.0409	5.1×10^{-5}	32.7
22.14	57	3.7679	3.7880	- 0.0201	13.9×10^{-5}	2.9
23.27	135	4.1186	4.1963	- 0.0777	4.2×10^{-5}	145.3
24.09	188	4.4524	4.4825	- 0.0301	3.3×10^{-5}	27.4
24.81	217	4.7304	4.7235	+ 0.0069	1.4×10^{-5}	3.3
24.84	141	4.7506	4.7334	+ 0.0172	3.7×10^{-5}	8.0
25.06	37	4.9044	4.8046	+ 0.0998	23.7×10^{-5}	42.0
25.06	84	4.8996	4.8046	+ 0.0950	7.9×10^{-5}	114.4
25.80	196	5.1440	5.0357	+ 0.1083	4.7×10^{-5}	247.8
26.92	104	5.3333	5.3578	- 0.0245	6.8×10^{-5}	8.8
27.68	148	5.6306	5.5560	+ 0.0746	16.9×10^{-5}	32.9
28.89	83	5.7604	5.8368	- 0.0764	20.4×10^{-5}	28.7
28.96	95	5.8038	5.8517	- 0.0479	10.8×10^{-5}	21.0
29.00	232	5.8343	5.8602	- 0.0259	6.1×10^{-5}	10.9
30.05	148	5.9630	6.0667	- 0.1037	13.0×10^{-5}	83.0
Total				- 0.0793		1052.6

χ^2 at $P = 0.05$ with 18 degrees of freedom = 28.9.

assumed that the mid point between the extremes of temperature fluctuation was equivalent to the mean temperature. If the temperature in the thermostats did not rise and fall at the same rate this may introduce an error that would be considerable with a wide range of temperature fluctuation. But in fact Powsner was able to reduce the extreme fluctuations to very small dimensions (between ± 0.1 and $\pm 0.05^\circ\text{C}$. in the thermostats). Furthermore, he measured his temperatures to the nearest 0.01°C . on standardized thermometers. He also found that the short-term fluctuations in the thermostats were not reflected in any temperature change that he could measure within the vials. In the data for *Gryllulus* the mean was again assumed to lie at the mid point between temperature extremes but the fluctuations were a little greater in some instances than they were in either of the other two sets of data, and the

error introduced by this method would be correspondingly greater. However, since the same kinds of thermostats were used in all this work, the displacement of the mean from the mid point would be in the same direction at all temperatures and this would tend to minimize any influence this error might have, since its influence is merely to move the curve along the temperature axis but not to alter its shape. Provided the displacement is equivalent at all temperatures this error has no influence on any conclusions regarding the goodness of fit of the curve. In the data for *Gryllulus* this is not so (Table 2) but the introduced errors are likely to be small and in any case the results corroborate those obtained from the other two sets of data.

Table 4 shows that in the data for *Calandra* the lowest temperature array, 15.2°C., made by far the greatest contribution to the value of χ^2 . This was also true when the data for moisture level II, presented by Birch (1944), were similarly analysed. This circumstance gave rise to some suspicion regarding the validity of including the 15.2°C. array in the analysis and it was decided to recalculate these data omitting this array. When this was done, again using the maximal likelihood solutions for the parameters in the logistic equation, it was found that χ^2 became insignificant ($P > 0.90$), indicating that the trend in the rate of development over this temperature range was expressed adequately by means of a logistic curve. A similar situation occurred with the data for moisture level II.

Now the 15.2°C. arrays were discarded from these analyses solely because they contributed the greatest proportion of the total value of χ^2 , and this is not a sufficient reason for their exclusion (Yates 1933). Nevertheless, Birch's Table 3 shows that the mortality at this temperature was considerably higher than at the other temperatures used in the calculation of the curves, and this may indicate that this temperature was causing interference with development or hatching and should therefore be excluded. This was not stated by Birch in his paper, and indeed he included these arrays in his analyses, but in a letter he informs me that he considers it likely.

In the data for the other two species there is no indication that the extreme temperatures used lay outside the limits of temperature at which development proceeded without interference, yet the calculated curves depart significantly from the observed points. Both these curves were calculated from a greater number of observed points than the data for *Calandra* and it is quite likely, since a logistic curve can be calculated to fit three points exactly, that the fit obtained for *Calandra* when the array at 15.2°C. was discarded, was due, to some extent, to the reduction in the number of points to which the curve was required to conform.

The question then remains to some extent an open one but it would seem that the weight of evidence indicates that the data are sufficiently precise to enable any statistically significant departure of observed points from a hypothetical curve to be regarded as real and to make it unlikely that the observed trend in rate of development with temperature can be expressed precisely by means of a logistic curve.

Powsner (1935), as well as measuring the time required by *Drosophila* to complete embryonic development and hatch at a series of constant temperatures, also measured the mean time taken to reach the pupal stage from egg-laying and the mean time required to complete the pupal period, each at a series of constant temperatures. From these data logistic curves have been calculated by the graphical method that can be drawn through the observed points for percentage development per hour for the periods "egg-to-pupa" and "egg-to-adult." (The mean "egg-to-adult" periods were obtained by adding the corrected mean duration of the "egg-to-pupa" period to the mean duration of the pupal period at the same temperatures. The variances of these means were obtained by adding the variances of the two periods. This procedure is justifiable since the duration of the two periods was not correlated.)

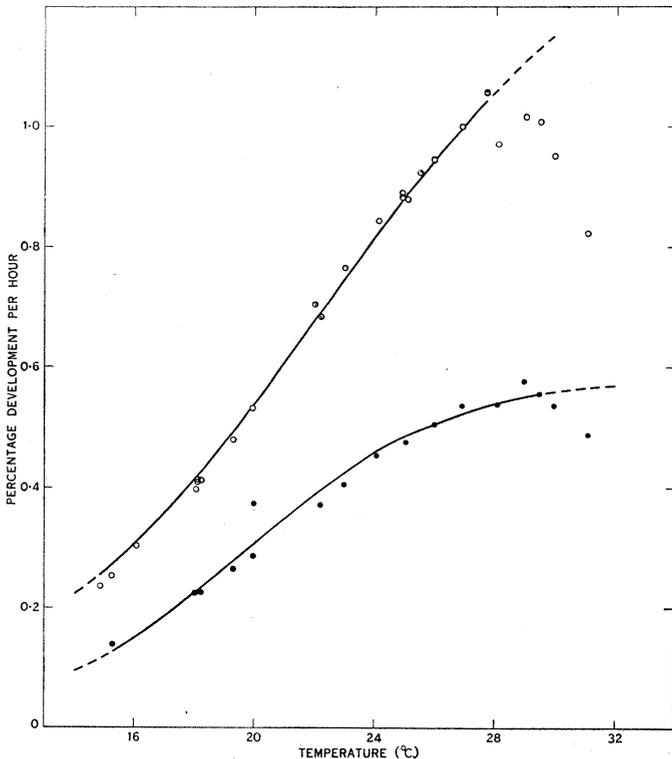


Fig. 4.—Logistic curves for the development of *Drosophila* drawn through the observed means. Upper curve, period of development from egg laying to pupation having the form

$$Y = \frac{1.376}{1 + e^{4.501606 - 0.203248t}}$$

lower curve, period of development from egg laying to adult emergence having the form

$$Y = \frac{0.587}{1 + e^{5.748103 - 0.292319t}}$$

Figure 4 shows these two curves drawn through the observed points, whilst Tables 6 and 7 show the calculations necessary to test the goodness of

fit of the two curves respectively. It can be seen on comparing these figures and tables with Figure 3 and Table 5 that the calculated logistic fits the data less and less well as the period of development under consideration is extended. Furthermore, the three periods of development show marked differences in their response to temperature; the optimum temperature for the egg stage being in the vicinity of 30°C., that for the egg-to-pupa stage about 27°C., and that for the egg-to-adult stage about 29°C. The points of inflexion of the three curves also differ markedly. Figure 5 shows the three curves drawn to the same scale and these differences can be clearly seen.

TABLE 6

GOODNESS OF FIT OF CALCULATED LOGISTIC CURVE FOR RATE OF DEVELOPMENT FROM EGG TO PUPA OF *DROSOPHILA MELANOGASTER* (DATA FROM POWSNER 1935)

Temp. (°C.)	<i>n</i>	\bar{y}_i	Y_i	$(\bar{y}_i - Y_i)$	s_i^2	χ^2
14.86	97	0.2365	0.2550	-0.0185	88×10^{-8}	388
15.24	227	0.2527	0.2714	-0.0187	32×10^{-8}	1097
16.06	148	0.3034	0.3095	-0.0061	70×10^{-8}	54
18.04	99	0.3987	0.4165	-0.0178	124×10^{-8}	255
18.05	423	0.4134	0.4171	-0.0037	30×10^{-8}	47
18.05	178	0.4100	0.4171	-0.0071	79×10^{-8}	63
18.21	81	0.4119	0.4266	-0.0147	153×10^{-8}	142
19.32	122	0.4803	0.4957	-0.0154	69×10^{-8}	343
19.97	125	0.5311	0.5383	-0.0072	401×10^{-8}	13
22.00	128	0.7052	0.6779	+0.0273	80×10^{-8}	935
22.00	195	0.7057	0.6779	+0.0279	109×10^{-8}	712
22.21	139	0.6840	0.6918	-0.0078	210×10^{-8}	28
22.99	220	0.7657	0.7470	+0.0187	124×10^{-8}	283
24.17	140	0.8439	0.8269	+0.0170	427×10^{-8}	67
24.93	242	0.8826	0.8778	+0.0048	119×10^{-8}	19
24.93	341	0.8913	0.8778	+0.0135	107×10^{-8}	170
25.14	1004	0.8795	0.8913	-0.0118	135×10^{-8}	102
25.56	357	0.9234	0.9177	+0.0056	142×10^{-8}	23
25.99	344	0.9479	0.9441	+0.0038	158×10^{-8}	9
26.89	185	1.0000	0.9964	+0.0036	225×10^{-8}	6
27.77	128	1.0860	1.0436	+0.0124	244×10^{-8}	63
27.77	192	1.0604	1.0436	+0.0169	214×10^{-8}	133
Total				+0.0227		4952

χ^2 at $P = 0.05$ with 19 degrees of freedom = 30.1.

The fit of the three curves shown in Figures 3 and 4 may also be regarded as becoming progressively better as the period of development considered becomes shorter and presumably less heterogeneous in nature. Thus in the data for the egg-to-adult period three distinct developmental stages, each differing to some extent in their response to temperature, have been added together and the composite trend with temperature was found to depart significantly from a logistic curve. Now even if the trend of each of the three stages could be expressed precisely by a logistic, it would only be possible to compound them and fit the result to a logistic if the parameters a and b in the three

separate logistic equations were identical. In this particular case this is not so (cf. Davidson 1944 for the equations for the development of the eggs and of the pupae of *Drosophila*). The curve for the development of the larval stage differs even more widely. Thus it is not justifiable to consider the total developmental period as a unit when attempting to express the trend in rate of development with temperature in the form of a logistic curve. This being so it seems probable that the several parts of embryogenesis will behave differently, one from another, in their response to temperature. Such differences have been shown for stages in the embryonic development of the frog *Rana pipiens* (Ryan 1941). This is further borne out by work on lethal or sublethal temperatures with *Drosophila* eggs, in which it was shown that the influence of temperature depended on the stage of development of the embryo (Powsner 1935, Table XVI).

TABLE 7

GOODNESS OF FIT OF CALCULATED LOGISTIC CURVE FOR RATE OF DEVELOPMENT FROM EGG TO ADULT OF *DROSOPHILA MELANOGASTER* (DATA FROM POWSNER 1935)

Temp. (°C.)	\bar{y}_i	Y_i	$(\bar{y}_i - Y_i)$	s_i^2	χ^2
15.24	0.1398	0.1267	+ 0.0132	4×10^{-8}	4350
18.05	0.2239	0.2255	- 0.0148	3×10^{-8}	7300
18.21	0.2266	0.2320	- 0.0055	16×10^{-8}	188
19.32	0.2643	0.2787	- 0.0144	8×10^{-8}	2588
19.97	0.2873	0.3066	- 0.0193	38×10^{-8}	982
20.00	0.3729	0.3079	+ 0.0650	10×10^{-8}	42300
22.21	0.3702	0.3972	- 0.0270	20×10^{-8}	3630
22.99	0.4063	0.4259	- 0.0196	12×10^{-8}	3192
24.17	0.4527	0.4629	- 0.0102	40×10^{-8}	263
25.14	0.4757	0.4884	- 0.0127	13×10^{-8}	1238
25.99	0.5057	0.5071	- 0.0014	9×10^{-8}	22
26.89	0.5338	0.5236	+ 0.0102	23×10^{-8}	452
28.07	0.5371	0.5406	- 0.0036	118×10^{-8}	11
28.99	0.5577	0.5509	+ 0.0068	72×10^{-8}	65
Total			- 0.0333		66581

χ^2 at $P = 0.05$ with 11 degrees of freedom = 19.7.

It may be that if a small part of embryogenesis could be studied (say the period from fertilization to the completion of the blastoderm) which could reasonably be supposed to show a uniform response to temperature throughout, then perhaps it would be possible to demonstrate that the trend in rate of development with change in temperature (using even more rigorous methods of assessing the actual temperatures), could be expressed precisely by means of a logistic curve. Atlas (1935) measured the change in rate of development with changing temperature of the period from fertilization to the first cleavage division of the eggs of *Rana pipiens* but since he presented his data in the form of a figure only they are quite unsuitable for use in testing the validity of the logistic curve (cf. also Ryan 1941).

As yet, however, there is no hypothetical nor philosophical reason for supposing that the trend in rate of development at different temperatures should conform to the logistic or to any other particular curve. Much more must be known about the physiology of development before a hypothesis that can then be tested empirically can be formulated on this question.

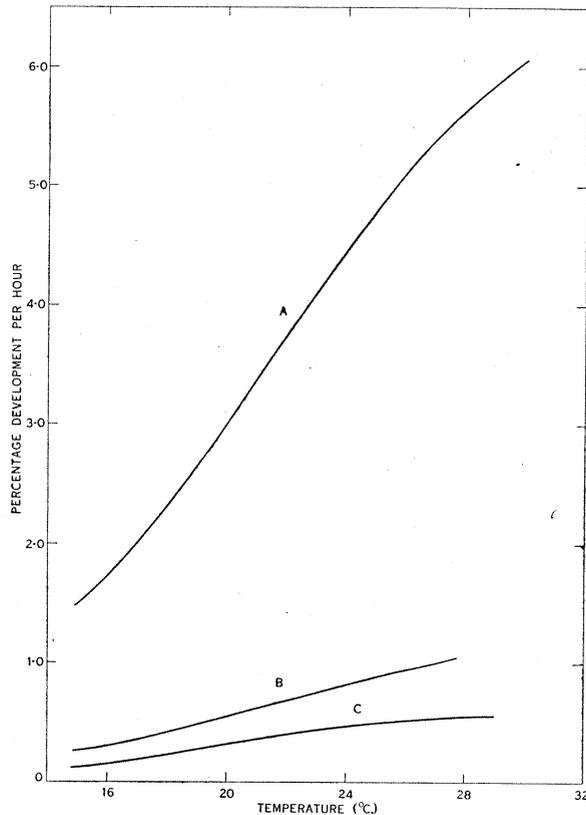


Fig. 5.—The three curves for the development of *Drosophila* drawn to the same scale.

A, development of eggs from laying to hatching.

B, development from egg laying to pupation.

C, development from egg laying to adult emergence.

From a physiological point of view then it remains an open question whether or not uniform stages of development, if such stages can be found, conform to the logistic in their trend in rate of development with temperature. It is certain, however, that if two or more such stages are considered together, the trend in their total development, supposing the several stages themselves show a logistic trend, cannot conform to a logistic curve unless they all respond in an identical manner to change in temperature (a and b in all the logistic equations must be identical).

From an ecological point of view, however, and it was as an ecologist that Davidson first proposed the use of the logistic, the logistic curve remains the most faithful representation of trend in rate of development of insects under changing temperature conditions. It can form a useful tool for predicting the rate of development at any particular temperature and the slight inaccuracies so introduced can be expected to be negligible when compared with the errors introduced by the estimations of field temperature unavoidable in ecological work.

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