Comparative studies on the developmental rates of the larvae of certain blowflies (diptera: calliphoridae) at constant and alternating temperatures

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Abstract

The four blowfly species (named below) were reared as larvae at constant 10°, 15°, 20° and 26° and alternating temperatures (12 hours/day at each) of 10° - 20° and 15° - 26°C.

Larval developmental zero temperatures calculated from the above constant temperatures data were as follows:-

Calliphora vicina R-D, 4.8°C; Calliphora vomitoria L, 5.7°C; Lucilia sericata Meig. and Phormia terrae-novae R-D. both 10.1°C. Calculated thermal (day-degree) requirements were also obtained for egg incubation and development of each larval instar for the 4 species. The temperatures or ranges within which each species completed larval development at the lowest day-degree figure, considered to be their most favourable temperatures, for each species were:- C. vicina, constant 10° and 15°C; C. vomitoria alternating 10° - 20°C; L. sericata had uniform thermal requirement at 15°, 20° and 26°C, but at 10°C failed to develop beyond the 1st/2nd instar moult: in P. terrae-novae the most favourable temperature was 26°C, failing to develop beyond the 2nd/3rd instar moult at 10°C.

Growth rate variation was found to be great within batches of larvae hatched within 30 minutes and reared on excess liver, and weighed at intervals. This variation in C. vicina and C. vomitoria was greater and produced higher S.E.'s at constant than at alternating temperatures, while in L. sericata this effect was not noticeable. In Phormia the S.E. was markedly inversely related to the temperature used.

Analysis of growth rate variation in the batches show that there were faster and slower developing individuals with corresponding gradation of final weights achieved, showing that slower developing larvae in the main failed to catch up with the faster larvae. The significance of these variations is discussed.

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Introduction

The aim of this investigation is to quantify the development of the egg, 1st instar, 2nd instar and 3rd instar of four species of blow-fly; Calliphora vicina R.-D., Calliphora vomitoria L., Lucilia sericata Meig. and Phormia terrae-novae R.-D., at various temperatures encountered during their development. The development is measured by the increase in live weight in a known time period for several constant and alternating temperature conditions.

There has been some lack of uniformity in previous investigations measuring larval development. Many workers, such as Peairs (1927) and Kamal (1958), who determined development by comparing larval duration against temperature, while others such as Putman (1977) and Hanski (1976a, 1977) determined development as an increase in weight of larvae over a known time period against temperature.

Peairs (1927) did not weigh the larvae but determined development as larval duration against temperature, and did not divide larval development into 1st, 2nd and 3rd instars, although he did point out the importance of determining the zero temperature for development, i.e. the temperature below which development did not occur, which is usually different between species.

Kamal (1958) determined development by the same method as Peairs (1927), but he did divide larval development into 1st, 2nd and 3rd instars, although his study was carried out at only one temperature.

Hanski (1976 , 1977) determined development as an increase in live weight over a known time period against various constant and alternating temperatures, but unfortunately he used very small numbers of larvae, starting at 100 larvae and reducing them to 5 as the larvae grew, and he did not divide larval development into 1st, 2nd and 3rd instars.

The fact that most workers did not divide the larval development into the various instars is unfortunate, as one might not expect the different instars to react to the same temperature in the same manner. More surprisingly is that the concept of a zero temperature for development has not been used by many authors after Pearis (1927), although it is obvious that each species must have a temperature below which they will not develop, and that this 'zero' temperature is unlikely to be the same for different species. I appreciate that these authors did not use the concept of a zero temperature of development because they were only interested in development at relatively high temperatures, well above the developmental zero. Even when comparing one or more species at relatively high temperatures, the zero temperature for development is still very important, because one can then compare the day-degrees above the 'zero' temperature required by each species for complete development, and hence obtain a quantitative comparison.

Using Pearis concept of a zero temperature for development, and knowing the period of time the larvae took to develop at a given temperature, one can then calculate how many day-degrees each egg or larval stage requires for its complete development. Although calculating and using day-degrees assumes that rates of development are linearly related to temperature, even though this may not actually be the case. However, day-degrees are useful as an approximation so that one can make a direct comparison of any given species or stage at several constant or alternating temperatures, and between different species at the same temperature.

These four species were selected for this study because they are insects that in general are thought to develop fairly rapidly as they live in dead carcasses in nature, which are temporary, so

each species requires a fairly rapid development to compete for this food source,(Hepburn 1943). I was further interested to compare blow-fly development with other insect development studies in general.

The results from my experiments, explained in the following text, show how each of the four species researched in this study has a temperature or temperature range to which it is best adapted, i.e. the temperature at which the species requires the least number of day-degrees to complete its development. This is best shown by using the zero temperature for development and day-degree concept as used by L.M. Peairs (1927), with the addition of dividing the larval development, by its natural division, into 1st, 2nd and 3rd instars.

Materials and Methods.

(1) General.

The larvae of *C. vicina*, *C. vomitoria*, *L. sericata* and *P. terrae-novae* used in these experiments were reared from eggs laid by fly cultures maintained in the laboratory at 22°C. These cultures were fed on a diet of sucrose and water, with ox liver as a protein source and oviposition site.

The eggs were collected from each fly culture by placing a piece of fresh ox liver in the cage and observing the liver at the end of each hour period. Only when sufficient eggs were laid within a single hour period were they used, and the mid-point of the hour was taken as the time of laying. These eggs were then placed on a moist glass slide contained in a petri dish, which had a wet filter paper on the bottom to keep the relative humidity high. This is because the survival of the egg stage declines rapidly with increasing saturation deficits, primarily through the inability of the larvae to rupture the chorion of the egg, (Vogt and Woodburn (1980) on *Lucilia cuprina* and Davies (1950) on *L. sericata* (Meigen) and other blowfly species).

These petri dishes containing the eggs were placed in the appropriate constant temperature room, 10°C, 15°C, 20°C and 26°C, and observed every half hour to determine the hatching time. Only the larvae hatching in the first half hour period, of hatching, were used in the experiments. This method gave a minimum hatching time rather than an average hatching time.

In all cases 50 - 100 larvae were transferred to, and reared on an excess of ox liver, this being the better medium compared to proteins of lower vertebrates, (Kozhanchikov 1947), which were reported to retard development and increase mortality. These larval

cultures were maintained in glass containers, 10cm in diameter and 7.5cm deep, which contained two wet filter papers with an excess of liver placed over them. Both the liver and filter papers were kept constantly wet in order to keep the relative humidity high; these containers were then covered with tissue paper to allow gaseous exchange, but stopping possible cross infection of the cultures, or larval escapes. The temperatures throughout all experiments will be given in degrees Centigrade or Celsius.

(2) Experiments at Constant Temperatures.

The larval sets were then kept in various constant temperature rooms, at 10°, 15°, 20° and 26° maintained at $\pm$ 0.5°.

These larvae were then weighed at appropriate time intervals by removing them from the liver, drying them quickly by rolling on filter paper, and taking the individual live weights, after which they were replaced on the liver in the containers and returned to the constant temperature rooms. This procedure was repeated throughout the larval development until after the maximum mean weight was achieved. This method was similar to that used by Hanski (1976a) on Lucilia illustris, where the increase in biomass was obtained from the difference between two successive measurements in weight. I encountered the same problems as Hanski (1976a) and followed similar practices:-

(i) The weight of the moulted cuticle, which usually has to be taken into account was disregarded here because it was negligible and not detectable when dealing with a population of larvae;

(ii) In most production studies the weight of the food in the intestine is a serious problem, so if we suppose that the relative weight of the food in the intestine is nearly constant throughout development, then it has little affect on the measured rate of development, only on the absolute weights;

(iii) In these experiments the heating effect of the larvae on their food was not considered to be of major importance, because of the relatively small number of larvae, 50 - 100, present compared to the amount of liver, which was always in excess, although in nature this effect may be considerable. It was shown by Deonier (1940) on the winter populations of several species of blowfly, that smaller carcasses, such as those of jackrabbits, lambs, cats and small dogs, were not found to develop or hold a temperature significantly above that of the atmosphere. Large carcasses such as those of sheep, goats, cattle and horses did develop temperatures significantly above that of the atmosphere.

(iv) When the time to maximum mean larval weight is taken from the graphs and tables produced, the time taken is at the top of the slope (steep), as arrowed in Fig2, Page IIa and an increase in the mean live weight of about 1mg over the next day or so was not classed as a significant weight increase at this point.

During the larval development the duration of the 1st and 2nd instars were determined by observing a sample of the larvae, namely 20 individuals, in each set at half hour intervals, and determining the instars present. The change from 1st to 2nd instar and 2nd to 3rd instar was noted when 10% of the larvae in each sample had moulted.* The moult from 1st to 2nd instar was noted by the significant lengthening of the basal sclerite in the cephalo-pharyngeal skeleton, and the 2nd to 3rd instar moult by the replacement of the small posterior spiracle with two slits, by a much larger spiracle with three slits in the 3rd instar.

These procedures were carried out at the constant temperatures of 10°, 15°, 20° and 26° for all four of the species previously mentioned. After the larvae had reached their maximum mean weight they were given access to moist peat in which to pupate, and the emmerging flies were used to maintain the laboratory cultures.

* Because at the 50% point some laggards, as mentioned later,

(3) Experiments at alternating temperatures

The same procedures were used for the experiments under conditions of alternating temperatures, except that the cultures were moved from one temperature to the other at 12 hour intervals as outlined below. The temperatures used for C. vicina were 5° - 15°, 10° - 20° and 15° - 26°, and for C. vomitoria, L. sericata and P. terrae-novae 10° - 20° and 15° - 26°.

These experiments were run, similar to those of Hanaki (1977) on Lucilia illustris, to assess to what extent the actual and predicted, from the constant temperature experiments, developmental rates coincide with each other at alternating temperature conditions.

The eggs for the alternation of temperature experiments were collected around mid-day, because these species seemed usually to lay their eggs during the day time. These were then divided into three batches in C. vicina, and into two batches in C. vomitoria, L. sericata and P. terrae-novae, for the different alternating temperature conditions as specified above.

Each batch of eggs, laid in the late morning or early afternoon, was then placed at the higher of the two temperatures used in each experiment, the higher temperature approximately simulating daytime and the lower night-time, until 9.00 p.m., and were then transferred to the lower temperature. From then on they alternated at 12 hour intervals between these two temperatures, being weighed at the end of each 12 hours to determine the weight increase and hence the growth; but in each case the weighing did not start until around the 2nd instar. This was because (a) the larvae are very small and the weight increase is proportionally small, and hence subject to weighing error, (b) the larvae when small are very susceptible to dessication, (c) the development of the 1st and 2nd instars is more accurately measured by the duration of the instars.

(4) Control experiments to determine the effects of handling and weighing on larval growth and mortality.

Two control experiments were carried out at a constant 26° using C. vicina and C. vomitoria to see if the handling procedure had any affects on the rate of development, or on the maximum mean larval weight achieved, or on mortality.

For each species a batch of eggs was split into four approximately equal sets, which were then hatched by the procedure mentioned previously. Then two sets were weighed regularly all the way through larval development, and the other two sets were not. When the sets that had been weighed all the way through had reached the maximum mean larval weight, then the number of larvae in these sets that had emptied their crops were counted. This is a good measure of their having reached complete development. Then the previously unweighed sets were weighed and the number of larvae in these sets that had emptied their crops were counted. Then the mean weights, and the number of larvae that had emptied their crops were compared to see if there was any significant difference between the weighed and unweighed sets, in rate of development and final mean weight.

Control experiments to determine if the handling procedures used affected developmental rates, maximum mean weight or mortality.

Four sets were reared under the conditions stated previously, pages 5-6, at a constant 26° for both C. vicina and C. vomitoria, two of these sets were weighed at 24 hour intervals during larval development, and the other two were not touched during development, except by adding water to keep the relative humidity high. When the sets that were weighed throughout their development had achieved their maximum mean weight, then the untouched sets were removed from the liver and their mean weight determined.

A comparison of the data accumulated from these control experiments is laid out on Fig. 1a, 1b and Table 1a and 1b, from these one can see that in the cases of both C. vicina and C. vomitoria that the maximum mean weights achieved by both the periodically weighed and untouched larvae are very similar, and any slight differences could be accounted for by (i) slight genetic variations between batches of eggs; (ii) inevitable differences in the quality of liver supplied.

To check that the sets of larvae were all at about the same stage of development, the number of larvae with empty guts were counted in each set, (table 1a and 1b). This showed that there was no obvious differences between the weighed and untouched sets, in the cases of C. vicina and C. vomitoria.

Since a known number of larvae had been used for each set, I counted the number of larvae surviving to the end of larval development to see if the handling procedure increased mortality, there was no trend to suggest this, as shown on tables 1a and 1b. The above checks show that the procedures used in these experiments did not affect weight gains, final weights, development times or mortality.

Table 1a - Control experiment with C. vicina larvae reared at a constant 26°.

1 and 2 are the sets weighed periodically during development until all the larvae had pupated, as shown on Fig. 1a.

3 and 4 are the unweighed checks. All four sets were started with 100 newly hatched larvae.

The following results were obtained 4.19 days after hatching.

Set No.	max. mean weight of larvae (mgm)	% with empty guts	% Survival	No. of surviving larvae	
1	76.3	43.7	80	80	$\chi^2 = .01$ n.s.
2	84.2	50.6	79	79	
3	86.0	41.1	90	90	
4	81.7	42.9	77	77	

Table 1b - Control experiment with C. vomitoria larvae reared at a constant 26°.

1 and 2 are the sets weighed periodically during development until all the larvae had pupated, as shown on Fig. 1b.

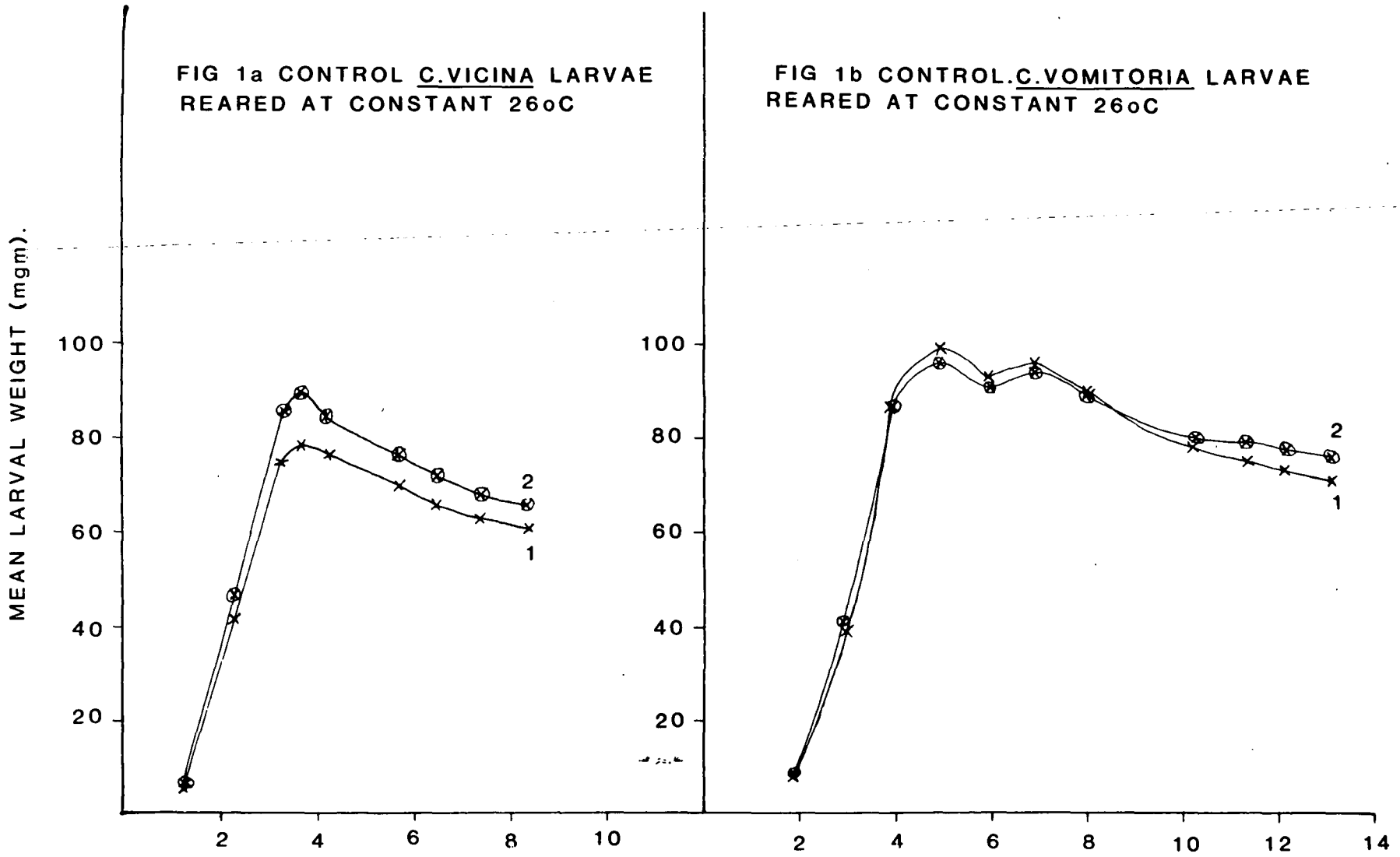
3 and 4 are the unweighed checks. All four sets were started with 75 newly hatched larvae.

The following results were obtained 5.94 days after hatching.

Set No.	Max. mean weight of larvae (mgm)	% with empty guts	% Survival	No. of surviving larvae	
1	93.2	51.4	47	35	$\chi^2 = 1.34$ n.s.
2	90.8	35.3	68	51	
3	92.3	27.8	31	23	
4	96.4	39.6	71	53	

FIG 1a CONTROL C.VICINA LARVAE REARED AT CONSTANT 26oC

FIG 1b CONTROL.C.VOMITORIA LARVAE REARED AT CONSTANT 26oC



Development of Calliphora vicina larvae at constant temperatures, 10°, 15°, 20° and 26°.

As expected, it can be seen from Fig.2 that the rate of larval development in C. vicina increases with an increase in temperature, within the range of constant temperature conditions used, and the optimum temperature for larval development must be at or above 26°. This may be the optimum temperature for the rate of larval development, but is not necessarily the optimum temperature for survival. It was shown by Tauthong and Brust (1976) on Aedes campestris, that the optimum temperature for survival was some degrees below that of the temperature they found gave the shortest developmental times.

It can be seen in Fig. 2 that the mean weight of the larvae increases with time to a maximum mean weight, after which the mean weight falls. This is due among other things, to the larvae emptying their guts as they enter into the prepupal stage. The heterogeneity in the final mean weights (maximum), at each temperature, were probably not due or related to temperature or to differences in the handling procedure, which suggests that they are due to either inevitable differences in the quality of liver supplied or slight genetic differences between batches of eggs. This variability in final weight was also found by Smith (1936) working on C. vicina, where the larvae reared on frog muscle under identical conditions showed a heterogeneity in maximum mean weights. Hanski (1976a and 1977) on Lucilia illustris found that the heterogeneity in maximum mean weight of the larvae reared under different temperature conditions was not related to temperature, and apparently varied at random.

It can be seen from Fig. 2 and Tables 2-5 that in C. vicina the standard error (S.E.) first of all increases as the mean larval weight increases, and then gets smaller after the maximum mean weight

FIG 2 C.VICINA, LARVAL DEVELOPMENT AT A CONSTANT 10oC, 15oC, 20oC AND 26oC.

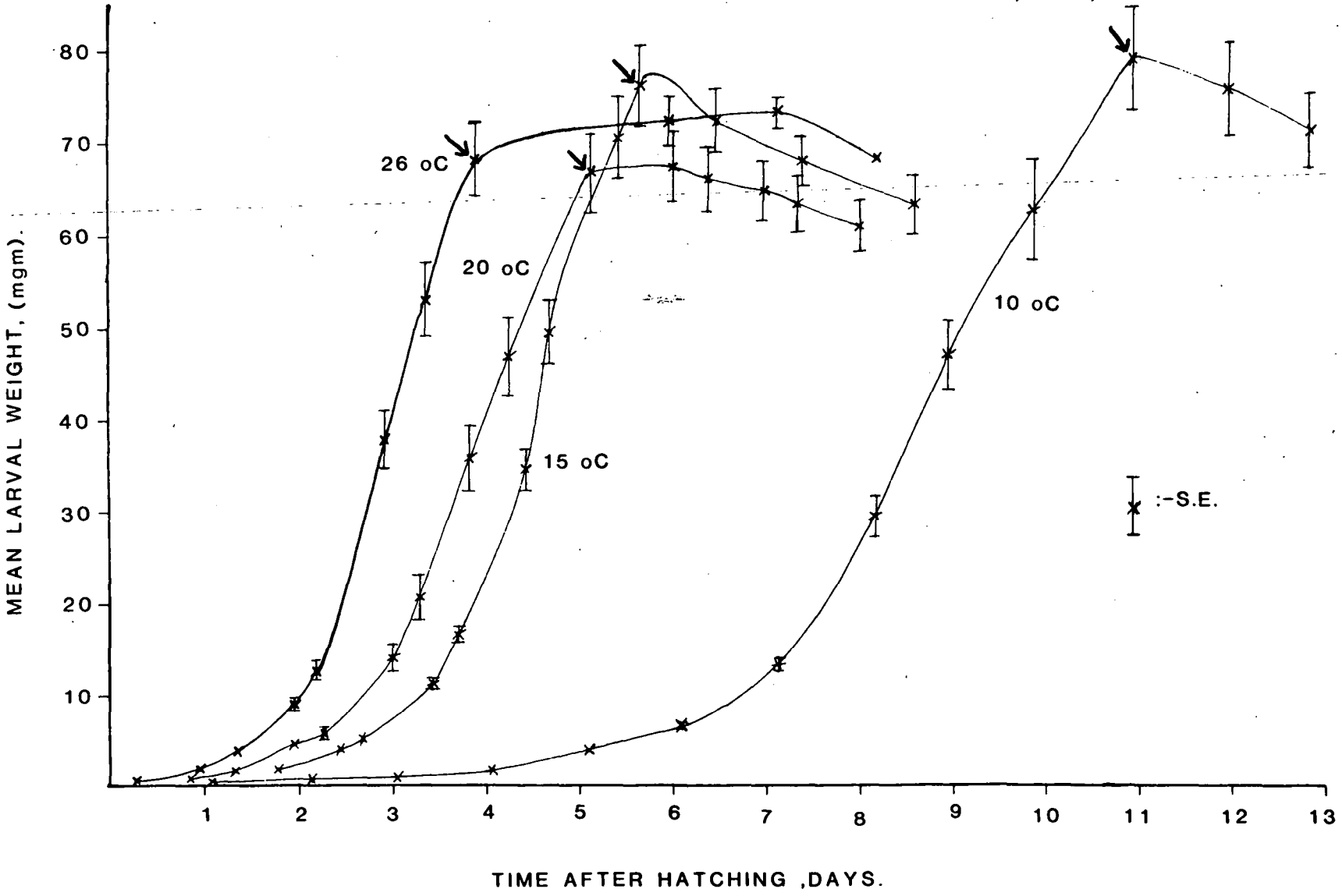


Table 2 *Calliphora vicina*, larval development as mean live weights (mgm) constant 26°C.

Time after hatching days	Mean Weight	Variance	S.D.	S.E.	Coefficient of variation %	No. Larvae
0.29	0.50	-	-	-	-	84
0.96	1.89	0.59	0.77	0.08	40.7	84
1.34	3.83	2.10	1.45	0.18	37.8	64
1.95	8.87	28.81	5.37	0.71	60.5	57
2.18	12.65	60.23	7.76	1.12	61.3	48
2.90	37.90	462.15	21.50	3.20	56.7	45
3.35	53.20	714.27	26.73	4.03	50.2	44
3.87	68.59	670.93	25.90	4.05	37.8	44
5.96	72.88	212.27	14.57	2.75	20.0	44
7.12	73.94	171.37	13.09	1.72	17.7	44
8.17	68.80	-	-	-	-	44

Table 3 *Calliphora vicina*, larval development as mean live weights (mgm) at constant 20°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
0.86	0.78	0.03	0.17	0.02	22.0	45
1.31	1.59	0.25	0.50	0.09	31.3	33
1.94	4.41	2.62	1.62	0.27	36.7	37
2.27	5.52	5.49	2.34	0.40	42.5	35
3.00	14.13	63.60	7.97	1.48	56.4	29
3.29	20.91	161.86	12.72	2.36	60.8	29
3.82	35.88	357.50	18.91	3.57	52.7	28
4.23	47.05	509.60	22.57	4.27	48.0	28
5.12	67.11	488.08	22.09	4.25	32.9	27
6.00	67.73	400.10	20.00	3.85	29.5	27
6.37	66.34	329.02	18.14	3.49	27.3	27
6.96	65.27	287.58	16.96	3.26	26.0	27
7.32	63.95	249.98	15.81	3.04	24.7	27
8.09	61.45	222.24	14.91	2.87	24.3	27

Table 4 *Calliphora vicina*, larval development as mean live weights (mgm) at constant 15°C.

Time after hatching days	Mean Weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
1.78	1.80	0.11	0.34	0.05	18.7	43
2.43	4.00	0.61	0.78	0.12	19.5	42
2.68	5.21	1.03	1.02	0.16	19.5	42
3.43	11.33	12.58	3.55	0.61	31.3	34
3.69	16.98	35.76	5.81	0.92	34.2	40
4.43	34.76	198.63	14.09	2.20	40.5	41
4.68	49.76	487.12	22.07	3.45	44.4	41
5.41	70.89	818.51	28.61	4.58	40.4	39
5.66	76.41	717.61	26.79	4.35	35.1	38
6.47	72.75	459.14	21.43	3.48	29.4	38
7.38	68.45	288.59	16.99	2.83	24.8	36
8.68	63.96	343.87	18.54	3.18	29.0	34

Table 5 *Calliphora vicina*, larval development as mean live weights (mgm) at constant 10°C.

Time after hatching days	Mean Weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
1.08	0.32	-	-	-	-	66
2.13	0.65	-	-	-	-	66
3.06	0.92	0.03	0.18	0.02	19.1	65
4.04	1.89	0.20	0.45	0.07	23.9	44
5.10	3.99	1.00	1.00	0.14	25.0	54
6.08	6.57	3.54	1.88	0.26	28.6	53
7.12	13.37	28.84	5.37	0.88	40.2	37
8.15	29.76	196.49	14.02	2.19	47.1	41
8.94	47.42	656.98	25.63	3.91	54.0	43
9.85	63.21	1304.51	36.12	5.51	57.1	43
10.92	79.81	1384.58	37.21	5.67	46.6	43
11.94	76.49	1092.21	33.05	5.10	43.2	42
12.81	72.05	719.06	26.82	4.19	37.2	41
15.85	58.80	427.07	20.67	3.31	35.1	39

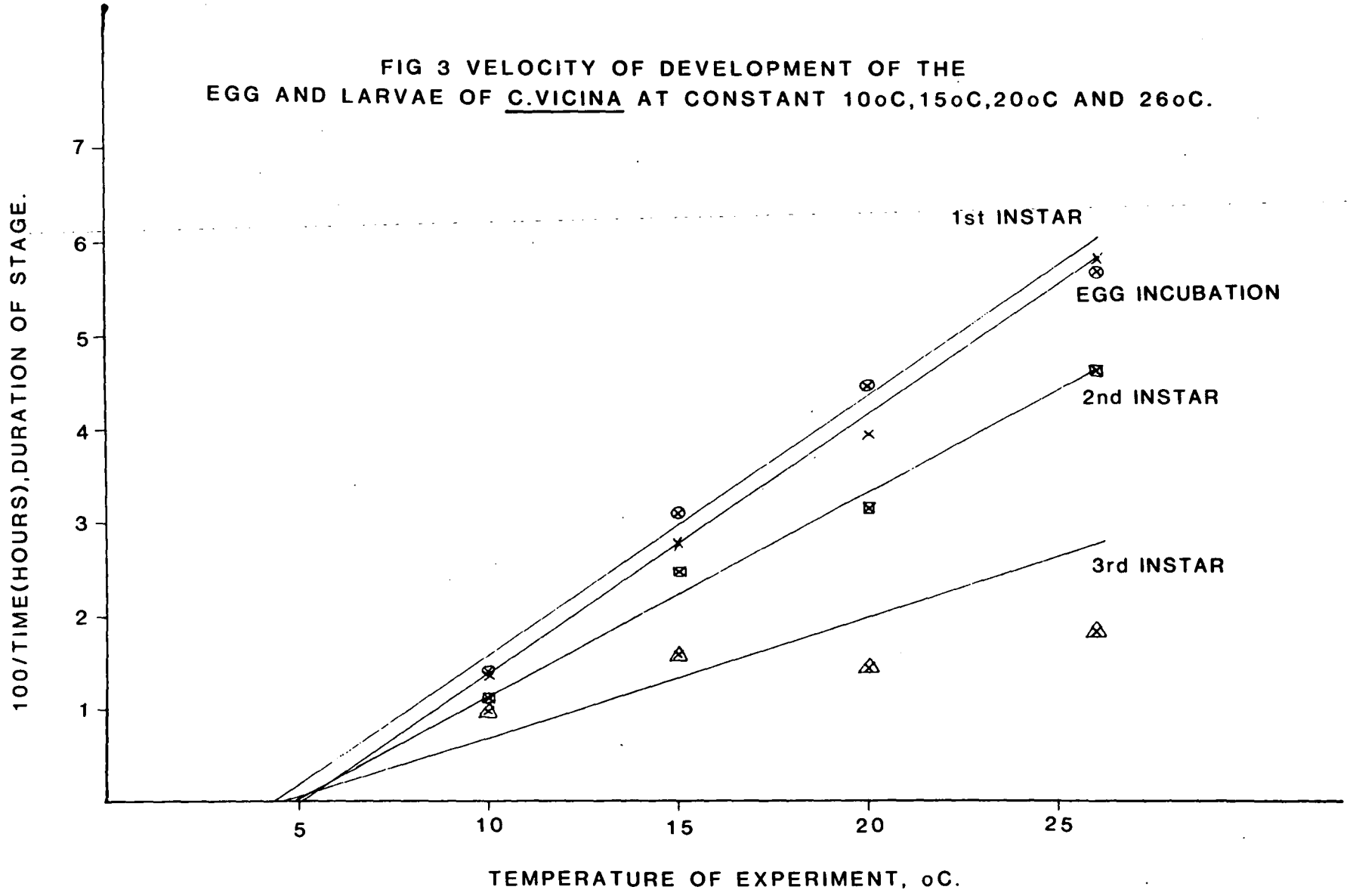
is reached. The more important aspect of the S.E., is that it gets smaller as the maximum mean weight is approached. This is when some larvae have stopped feeding, and have begun to empty their guts, as the rest of the population of larvae are still feeding and increasing in weight, so reducing the difference between individual weights. This is a good example of a rapid period of growth being staggered within a given population, and the fact that the S.E. continues to fall as the larvae enter into the prepupal stage, suggests a "Traffic-light" effect; i.e. there is a stage when faster developing larvae no longer change weight, or change very slowly, while slower developing larvae continue to change by growth and then slow up.

It is surprising that a population of larvae hatching at the same time, or within a time span of 30 minutes, and reared under identical conditions, should have such a heterogeneity in individual weights during much of the larval growth. But this could increase the survival rate of the population as a whole, as not all the larvae are at exactly the same stage of development until they reach the prepupal stage.

It appears from Fig. 2 that there is in C. vicina a disproportionate increase in the length of time of development of the larvae when the temperature is lowered from 15° to 10° as compared with the same 5° or 6° reduction from 26° to 20° and 20° to 15°, this is actually not the case, as discussed below.

When a velocity graph is plotted, as used by Pearis (1927) with various Lepidoptera, Coleoptera and Diptera, a zero for development can be extrapolated. The zero of the velocity graph is the point at which the line intersects the temperature axis. This is plotted for C. vicina in Fig. 3, where temperature is plotted against $\frac{100}{\text{time}}$ for each stage in hours (the lines being drawn in by eye). Unlike Pearis, the larval development was not taken as a whole, but was divided into egg incubation, 1st, 2nd and 3rd

FIG 3 VELOCITY OF DEVELOPMENT OF THE
EGG AND LARVAE OF C.VICINA AT CONSTANT 10oC,15oC,20oC AND 26oC.



instars, where the 3rd instar is the time between moulting from 2nd-3rd instars until maximum mean weight is achieved. It was divided into these stages of development, because as the physical and biochemical events that occur in these stages are so varied, it would be unrealistic to expect each stage to respond to a given temperature in the same way, and hence give the same extrapolated zero on the velocity graph.

Table 6 - Duration of egg and larval stages in the development of C. vicina, at the constant temperatures of 10°, 15°, 20° and 26°.

Constant temperature	Hatching Time (hrs.)	Duration of 1st Instar (hours)	Duration of 2nd Instar (hours)	Duration of 3rd Instar (hours)
10°	73.75	71.0	90.0	101.0
15°	36.0	32.25	40.5	63.0
20°	25.25	22.25	31.75	69.0
26°	17.08	17.5	21.5	54.0

As can be seen from Fig. 3, the extrapolated zero, read off Fig. 3 as drawn, lies between about 4.4° and 5.2°, and for further calculations I am going to use the median zero temperature of 4.8°. It is likely that the calculated developmental zero from Fig. 3 by extrapolation is higher than the real zero, as much previous work including that of Lin, S., Hodson, A.C. and Richards, A.G. (1954) on threshold temperatures for the development of Oncopeltus and Tribolium eggs, showed that the development velocity curve with temperature tends to flatten as zero is approached. So the real zero is probably lower than the extrapolated zero as drawn from a straight line on Fig. 3.

This zero temperature is used to calculate the day-degrees

required by each stage for full development, and for complete development from egg laying until maximum mean weight. A day-degree is defined as, one degree of temperature above the zero from the velocity graph for a period of 24 hours.

The day-degrees required by each stage are calculated by the following method:-

Duration of stage in days x degrees above zero from the velocity curve.

i.e. C. vicina at 15°

Duration of the 2nd instar is 40.5 hours = 1.69 days.

$15^{\circ} - 4.8^{\circ} = 10.2^{\circ}$ above zero from Fig. 3.

$\therefore$ Day-degrees = $1.69 \times 10.2^{\circ} = 17.2$ day-degrees (1 dec. place).

Table 7 - The day-degrees required by each stage at the four constant temperatures with C. vicina.

Temp. of experiment	Egg incubation	1st Instar	2nd Instar	3rd Instar	(Total) complete development egg laying → max. mean weight
10°	15.9	15.3	19.4	21.8	72.4
15°	15.3	13.7	17.2	26.8	73.0
20°	16.0	14.1	20.1	43.7	93.9
26°	15.1	15.4	19.0	47.7	97.2

It can be seen from Table 7, that egg incubation, 1st and 2nd instars each have their own thermal requirement for development in day-degrees, which is virtually constant for each of these stages and the variations are within the range of error of the observations at these temperatures,[1] This means that the fixed day-degree requirement determines the length of time each stage lasts at the temperatures used in these experiments. However the 3rd instar does not have a constant day-degree requirement, but as can be seen in Table 7

[1] see note on page 17.

increases with temperature. This means that the duration of the 3rd instar, at the temperatures used in these experiments, is not dependent on the day-degree requirement alone. There are several possible explanations for this unexpected result:-

1. Experimental error. This is extremely unlikely as the timings in these experiments for the 3rd instar at 10° would have to have been some 4.5 days out, and 1.75 days at 15°.

2. Slower development at higher temperatures, i.e. inhibition by high temperatures or stimulation by lower temperatures.

3. Temperature independence of development in the 3rd instar. This would explain the lower day-degree requirement at 15° and 10°, but would not explain the increase in time required by the 3rd instar at 10°; i.e. the 3rd instar takes 2.25 days (54 hrs.) at 26°, 2.875 days (69 hrs.) at 20°, 2.63 days (63.12 hrs.) at 15°, but 4.21 days (101.04 hrs.) at 10°.

4. Adaptation by C. vicina to develop comparatively quicker at the lower temperatures of 10° and 15°, which are conditions which they would encounter frequently in their natural enviroment. This is a strong possibility, but the difficult question is; why does this only occur in the 3rd instar and not in egg incubation and 1st and 2nd instars?

5. When one looks back at Table 6, it can be seen that the minimum time required for the development of the 3rd instar is 2.25 days, (54 hrs.) at 26°; and looking at Table 7 one can see that the minimum day-degree requirement for the development of the 3rd instar is about 22 day-degrees at 10°. Hence it appears as if there is a minimum time requirement, as well as a minimum day-degree requirement, i.e. about 22 day-degrees and a minimum period of about 2.25 days. This would explain the similar times of the 3rd instar at 26°, 20° and 15° of 2.25 days, 2.875 days and 2.63 days respectively.

Also it would explain the increase in time at 10° of 4.21 days, and the lower day-degree requirement.

The temperature time graph, Fig. 3, as used by Pearis (1927) and others, on the complete development of larvae or pupae of several insects, was applied by J. Davidson (1944) on the development of insect eggs at constant temperatures. Davidson showed by plotting $\frac{100}{\text{time}}$ in hours, i.e. 100 x the reciprocal of time, that this represented the average percentage development made by the embryo per hour, at the given temperature. More importantly he calculated an equation for the temperature/time curve, from which he could determine the temperature from a given value of $\frac{100}{\text{time}}$. This ability of being able to calculate the temperature, finds strong agreement with my findings, that in C. vicina the hatching, 1st and 2nd instars have a thermal requirement in day-degrees for their complete development.

It can be seen from my results for C. vicina calculated in day-degrees above the zero from the velocity graph, that the large time increase on Fig. 2 from 15°C to 10°C is as expected. Infact it is the 26°C and 20°C that are slower than expected, due to the increased time for the development of the 3rd instar. An equivalent graph to Fig. 2 was plotted by Hanski (1976) for Lucilia illustris at several constant temperatures. Hanski did not consider or calculate the zero from the velocity curve, but looked at development directly against temperature. He suggested that his calculations showed a slowness of growth at low temperatures early in development. Although I have done no work on Lucilia illustris, I would like to tentatively suggest that this may not actually be the case, and really before making this statement he should have sub-divided the larvae into 1st, 2nd and 3rd instars, and used the zero for development from the velocity curve. Hanski (1976) on Lucilia illustris, did however find

an indication that temperature dependence was more pronounced during this first 30 mg of weight curve, which is about the middle of the 3rd instar, than in the later stages. This is also shown by my day-degree results for C. vicina, where the 3rd instar development is not dependent on temperature alone.

Note on observational error.

Because the larvae hatched within a ½ hour period, and had been observed at ½ hour intervals for instar changes, the error could be 1 hour, which could give rise to an error of 4 to 5 %.

Individual live larval weight variations within each set of larvae of C. vicina, reared at the constant temperatures of 10°, 15°, 20° and 26°.

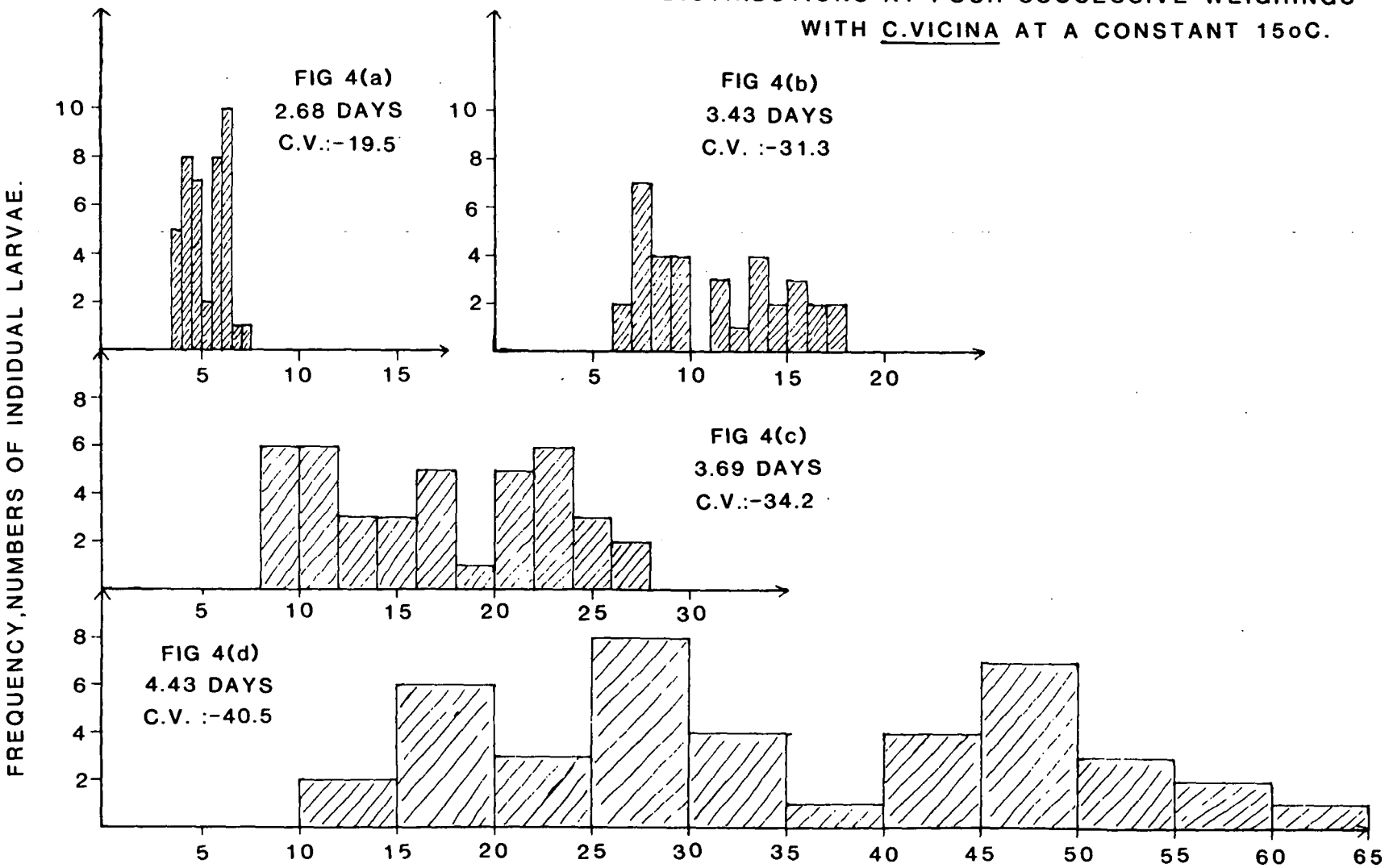
The previous data show the development of a population of larvae, but not the individual variations within a given population. If we wish to compare the scatter of different variables, in this case live weights, about their means, it is useful to be able to express the scatter in some form which is not dependent on the absolute size of the variables. This comparison may be usefully made by calculating the Coefficient of Variation at each weighing of the larvae, which is readily obtained by expressing the standard deviation as a percentage ratio of the mean; i.e. :-

$$\text{Coefficient of Variation (C.V.)} = \frac{100 \times \text{Standard Deviation}}{\text{Mean}}$$

Hanski (1976) with Lucilia illustris found a period of rapid growth in the early 3rd instar, and from his experiments concluded that assimilation and cumulative net production efficiency was generally maximal somewhere between the weights of 8 and 30 mg i.e. during the period when the growth rate was highest.

When we look at the results, Tables 2-5, and Fig. 4, a-c, for C. vicina we can see that there is a rapid period of growth of the larvae in the 3rd instar, the 2nd - 3rd instar moult occurs at a larval weight of about 9 mg. Looking more carefully at Fig. 4, a-c, one can see that as the larvae enter into this period of rapid growth, the C.V. increases rapidly as the frequency distributions widen on successive weighings. So an increasing C.V. indicates the beginning of a period of rapid growth, because larvae entering into this period surge ahead of larvae which have not yet entered into this period.

FIG 4a,b,c,d. FREQUENCY DISTRIBUTIONS AT FOUR SUCCESSIVE WEIGHINGS WITH C.VICINA AT A CONSTANT 15oC.



In the same manner, looking at Tables 2-5, one can see that as the increases between mean larval weights drop between successive weighings, that the C.V. starts to decrease. Hence a decreasing C.V. indicates that the larvae are approaching the end of a period of rapid growth, as the larvae coming out of this period begin to be caught up by those that are in or entering into the period of rapid growth.

On closer investigation of Tables 2-5 it becomes apparent that the timing of this rapid period of growth changes with temperature. As an arbitrary figure I calculated the range over which the C.V. was 75% of its maximum value, i.e. when the C.V. was high for each temperature. This gave the following results, showing the mean larval weights between which rapid growth occurred, at each of the four temperatures used, 10°, 15°, 20° and 26° with C. vicina.

10°C	29.76 mg	-	76.49 mg
15°C	16.98 mg	-	76.41 mg
20°C	14.13 mg	-	47.05 mg
26°C	8.87 mg	-	53.20 mg

These show that the period of rapid growth starts and finishes later at the lower temperatures, so lower temperatures delay or prolong this period of rapid growth.

Development of Calliphora vomitoria larvae at constant temperatures, 10°, 15°, 20° and 26°.

The developmental rates of C. vomitoria show an increase, Fig. 5, with an increase in the constant temperature, as found with C. vicina. Also as found with C. vicina, under constant temperature conditions, the developmental curve follows a sigmoid course, this type of curve was also found by Hanski (1976) with Lucilia illustris and by Putman (1977) on Calliphora erythrocephala = (C. vicina)

It can be seen in Fig. 5 that the mean weight of the larvae increases with time to a maximum mean weight, after which the mean weight falls, as found with C. vicina. This fall is due to, among other things, the fact that the larvae have stopped feeding and have begun to empty their guts. As with C. vicina I would suggest that the heterogeneity in the final mean weights (maximum), at each temperature, were probably not due or related to temperature or to differences in the handling procedure, but are due to either inevitable differences in the quality of liver supplied, or slight genetic differences between batches of eggs.

It can be seen from Tables 8-11 that with C. vomitoria, as with C. vicina, the S.E. first of all increases as the mean larval weight increases, and then decreases as the maximum mean weight is approached. As with C. vicina, I suggest that this occurrence with C. vomitoria will give rise to a "Traffic-light" effect as explained in the section for C. vicina, Page 12.

It appears from Fig. 5 that there is in C. vomitoria a disproportionate increase in the length of time of development of the larvae when the temperature is lowered from 15° to 10° as compared with the same 5° (or 6°) reduction from 26° to 20° and 20° to 15°, this is actually not the case, as discussed below.

FIG 5. C.VOMITORIA LARVAL DEVELOPMENT AT A CONSTANT 10oC,15oC,20oC AND 26oC.

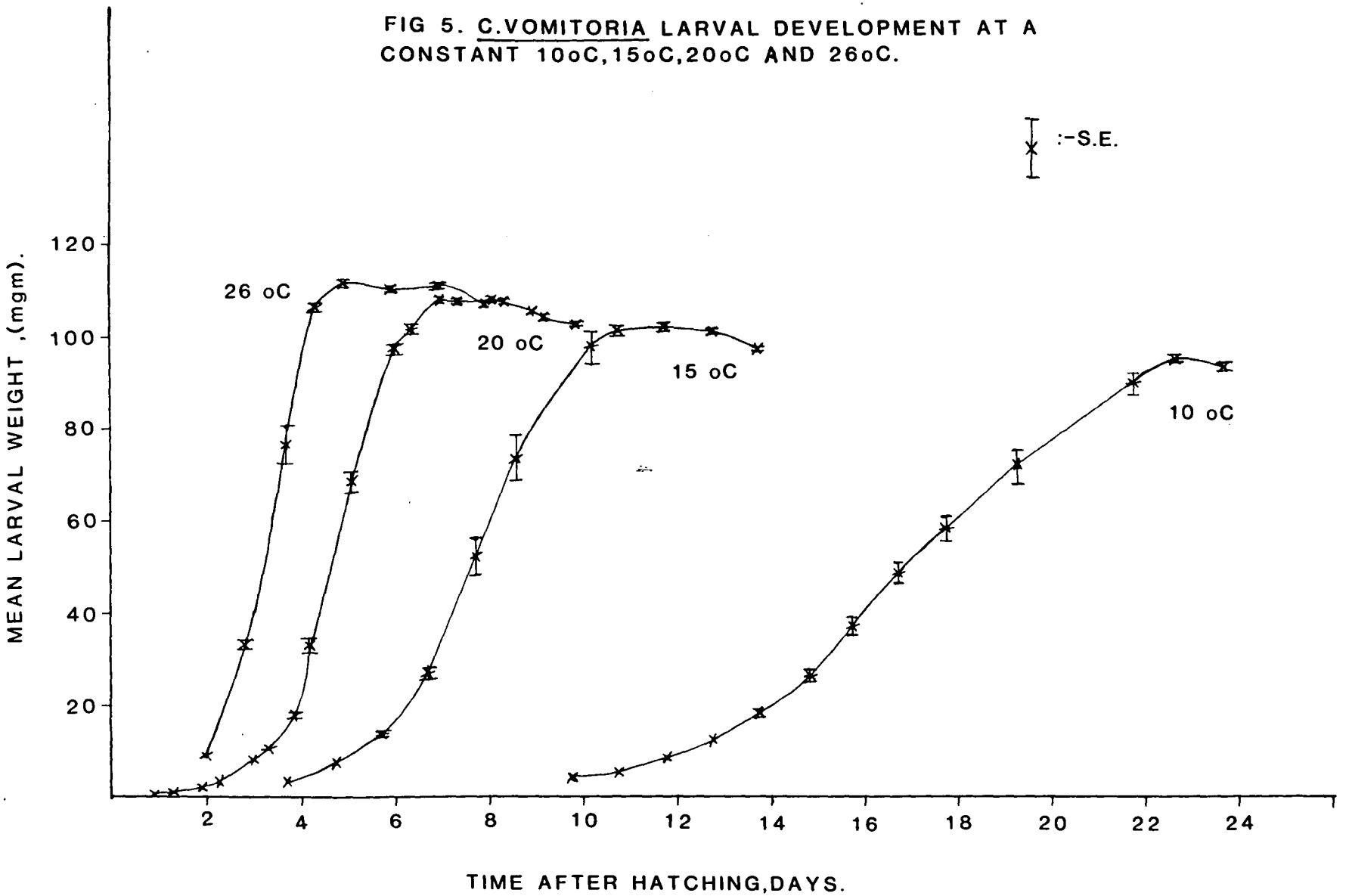


Table 8 *Calliphora vomitoria*, larval development as mean live weights (mgm) at constant 26°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
1.96	8.87	11.62	3.41	0.41	38.4	68
2.79	32.79	258.77	16.09	2.09	49.0	59
3.69	76.40	717.61	26.79	4.35	35.1	56
4.29	106.66	186.55	13.66	1.99	12.8	47
4.87	111.74	90.32	9.50	1.39	8.5	47
5.92	110.30	71.48	8.45	1.23	7.7	47
6.92	111.37	87.46	9.35	1.36	8.4	47
7.87	107.09	84.73	9.20	1.34	8.6	47

Table 9 *Calliphora vomitoria*, larval development as mean live weights (mgm) at constant 20°C.

Time after hatching days	Mean Weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
0.90	0.44	0.01	0.10	0.01	22.6	54
1.29	0.84	0.03	0.17	0.02	20.0	50
1.95	1.95	0.15	0.39	0.06	19.8	42
2.25	2.98	0.46	0.68	0.11	22.9	40
2.98	7.82	4.97	2.23	0.35	28.5	40
3.27	10.66	7.00	2.64	0.43	24.8	38
3.81	17.86	26.40	5.14	0.83	28.8	38
4.19	27.98	72.19	8.50	1.38	30.4	38
5.08	64.37	305.27	17.47	2.83	27.1	38
5.99	97.75	374.88	19.36	3.14	19.8	38
6.35	101.76	283.62	16.84	2.73	16.5	38
6.94	108.28	151.37	12.30	2.00	11.4	38
7.31	107.93	80.82	8.99	1.46	8.3	38
8.03	108.25	79.33	8.91	1.44	8.2	38
8.29	107.47	55.55	7.45	1.23	6.9	37
8.90	105.76	51.06	7.15	1.17	6.8	37
9.18	104.18	53.76	7.33	1.21	7.0	37
9.85	102.82	52.87	7.27	1.20	7.1	37

Table 10 Calliphora vomitoria, larval development as mean live weights (mgm) at constant 15°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
3.69	3.07	2.06	1.43	0.19	46.7	60
4.73	6.94	18.65	4.32	0.56	62.2	59
5.69	13.57	57.41	7.58	1.07	55.8	50
6.67	27.17	305.89	17.47	2.50	64.3	49
7.73	52.13	746.40	27.32	4.17	52.4	43
8.58	73.49	984.89	31.38	4.90	42.7	41
10.12	98.33	547.12	23.39	3.79	23.8	38
10.73	101.76	191.82	13.85	2.28	13.6	37
11.69	102.62	116.30	10.78	1.77	10.5	37
12.75	101.82	74.90	8.65	1.42	8.5	37
13.73	97.62	43.16	6.57	1.08	6.7	37

Table 11 Calliphora vomitoria, larval development as mean live weights (mgm) at constant 10°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
9.74	4.37	1.22	1.10	0.19	25.3	35
10.75	5.38	2.34	1.53	0.26	23.4	34
11.77	8.67	4.87	2.21	0.39	25.4	32
12.75	12.47	11.85	3.44	0.61	27.6	32
13.71	18.41	38.34	6.19	1.15	33.6	29
14.81	26.46	85.50	9.25	1.72	34.9	29
15.71	37.54	144.26	12.01	2.23	32.0	29
16.70	48.90	187.71	13.70	2.59	28.0	28
17.67	58.86	300.28	17.33	3.27	29.4	28
19.21	72.93	387.50	19.68	3.79	27.0	27
21.69	90.82	259.30	16.10	3.16	17.7	26
22.60	96.04	153.24	12.38	2.43	12.9	26
23.65	94.47	125.21	11.19	2.19	11.8	26

The data was handled as for C. vicina as described on pages 13 and 14, so when a velocity graph is plotted, as used by Pearis (1927), a zero for development can be extrapolated.

This is plotted for C. vomitoria in Fig. 6, where temperature is plotted against $\frac{100}{\text{time}}$ for each stage in hours, the lines being drawn in by eye.

Table 12 - Duration of egg and larval stages in the development of C. vomitoria at the constant temperatures of 10°, 15°, 20° and 26°.

Constant temp.	Hatching time (hours)	Duration of 1st instar (hours)	Duration of 2nd instar (hours)	Duration of 3rd instar (hours)
10°	75.5	147.5	144.5	250.5
15°	46.0	63.0	64.5	130.0
20°	24.25	38.0	47.5	81.0
26°	17.5	24.5	28.5	64.0

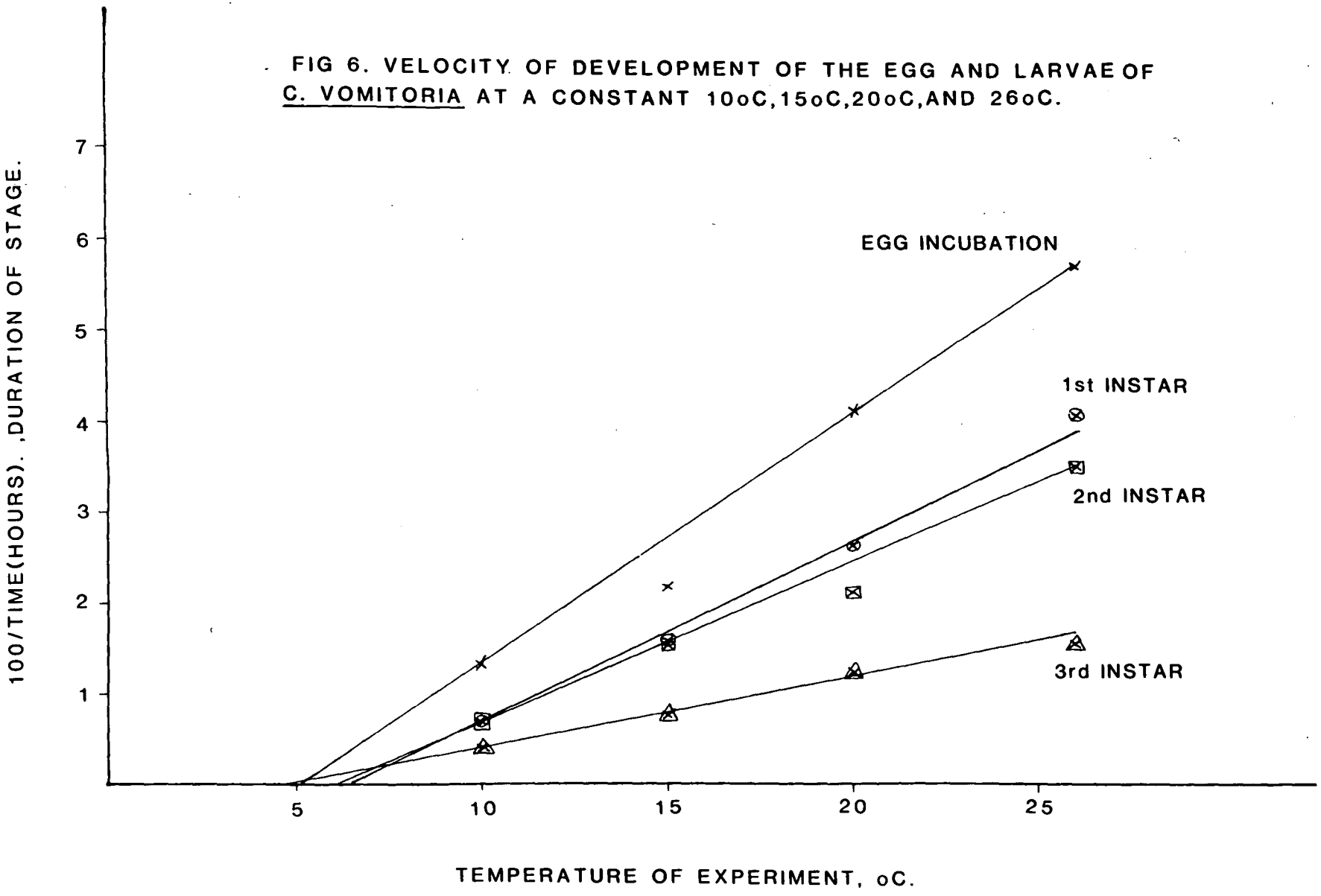
As can be seen from Fig. 6 the extrapolated zero, read off from Fig. 5, lies between 4.9° and 6.5°, and for further calculations 5.7° is used.

This zero temperature was then used to calculate the day-degrees required by each stage as with C. vicina.

Table 13 - Day-degrees required by each stage at the four constant temperatures, 10°, 15°, 20° and 26° with C. vomitoria.

Temp. of experiment	Egg incubation	1st instar	2nd instar	3rd instar	(Total) complete development egg laying → max. mean weight
10°	13.6	26.5	26.0	45.1	111.2
15°	17.9	24.4	25.0	50.4	117.7
20°	14.5	22.7	28.3	48.3	113.8
26°	14.8	20.7	24.1	54.2	113.8

FIG 6. VELOCITY OF DEVELOPMENT OF THE EGG AND LARVAE OF C. VOMITORIA AT A CONSTANT 10oC,15oC,20oC,AND 26oC.



It can be seen on Table 13, that egg incubation, 1st, 2nd and 3rd instars each have their own thermal requirement in day-degrees, which is fairly constant, allowing for experimental error, for each of these stages. This means that the day-degree requirement determines the length of time each stage lasts, and hence the time for complete development, at the temperatures used in these experiments. A similar result for C. vomitoria was discovered by a different method by Peairs (1927) with C. vomitoria pupae. He found the CO_2 production at 7°, which he had found to be the zero of the velocity curve, and called this the constant daily basal metabolism. He then found the CO_2 production at 10°, 20° and 30° for the complete development of the pupae, and then subtracted the basal metabolism, from this he found that the CO_2 production was constant.

This offered no difficulty in the way of the acceptance of the thermal constant as indicating that the processes of development represent a definite total of metabolic activity, which may require a definite amount of heat for its accomplishment.

Further verification of this was found by Davidson (1944) as previously discussed on page 16. The findings of Peairs, Davidson and myself suggest that the egg to pupal development of C. vomitoria requires a thermal constant above the zero for development from the velocity graph.

When one compares the duration of the four stages of C. vicina and C. vomitoria in Tables 6 and 12, one can see that the egg incubation times of C. vomitoria and C. vicina are very similar except at 15°. This was also the case found by Kamal (1958) on his study of 11 species that included C. vicina and C. vomitoria. Kamal (1958) found that the duration of the first instars of C. vicina and C. vomitoria were very similar, in my study I found there was a significant difference. In C. vicina the duration of the first instar was about the same length as the egg

incubation time at each temperature, whereas in C. vomitoria the duration of the first instar was about 1.5 x the egg incubation time at 15°, 20° and 26°, and about 2 x at 10°. This shows the much longer development of C. vomitoria which is perpetuated throughout the larval development, at all temperatures used in this work. I do however agree with Kamal's findings that the 2nd and 3rd instars of C. vicina are of much shorter duration than those of C. vomitoria, and that thus overall C. vicina develops in a shorter period of time.

A similar situation to the above was demonstrated by Ash and Greenberg (1975) between two related species, where they found Phaenicia sericata = (L. sericata) required a longer period to develop, at both low and high temperatures, than Phaenicia pallescens.

Individual live larval weight variations within each set of larvae of C. vomitoria, reared at the constant temperatures of 10°, 15°, 20° and 26°.

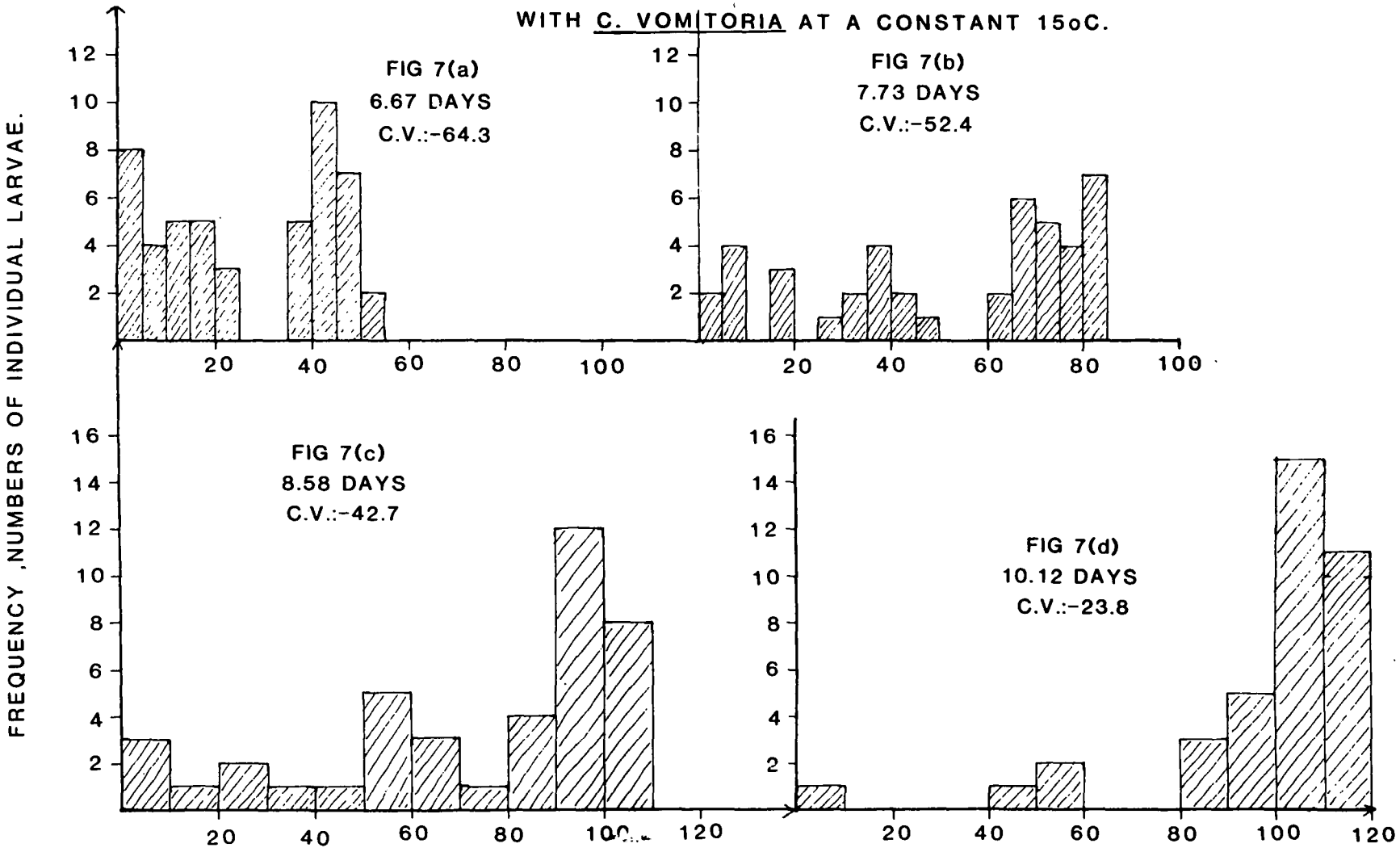
Looking at Fig. 7 a-d one can see that as the larvae approach the end of the period of rapid growth, the C.V. decreases rapidly as the frequency distributions become narrower on successive weighings. So a decreasing C.V. indicates the end of a period of rapid growth, as the larvae coming out of this period begin to be caught up by those that are in, or entering into, the period of rapid growth. In the same manner, looking at Tables 8-11, one can see that as the increases between mean larval weights increase, between successive weighings, that the C.V. starts to increase. Hence a rapidly increasing C.V. indicates that the larvae are entering into, or have entered into, a period of rapid growth.

As an arbitrary figure I calculated the range over which the C.V. was 75% of its maximum value, i.e. when the C.V. was high for each temperature. This gave the following results, showing the mean larval weights between which rapid growth occurred, at each of the four temperatures used, 10°, 15°, 20° and 26° with C. vomitoria, from Tables 8-11.

10°	5.38 mg	-	72.99 mg
15°	6.94 mg	-	52.41 mg (above)
20°	2.98 mg	-	64.37 mg
26°	8.87 mg	-	76.40 mg

These results are quite different from those found from C. vicina, in that the rapid period of growth starts much earlier; with C vomitoria this rapid period of growth starts somewhere between 3-9 mg, whereas with C. vicina it starts between 9-30 mg depending on the temperature. So with C. vomitoria this rapid period of growth extends over a greater

FIG 7 a,b,c,d. FREQUENCY DISTRIBUTIONS AT FOUR SUCCESSIVE WEIGHINGS WITH C. VOMITORIA AT A CONSTANT 15oC.



period of the larval development, and its timing is unaffected by different temperatures in C. vomitoria. This means that the rapid period of growth in C. vicina starts at the early 3rd instar, but in C. vomitoria it starts at the early 2nd instar and continues through until around the middle of the 3rd instar. In C. vomitoria the 1st - 2nd instar moult occurring at about 1.5 mg, and the 2nd - 3rd instar moult at about 16.0 mg, whereas with C. vicina the 1st - 2nd instar moult occurs at about 2.0 mg, and the 2nd - 3rd instar moult at about 9 mg.

Development of Lucilia sericata larvae at constant temperatures, 10°, 15°, 20° and 26°.

As with the Calliphora species, L. sericata developmental rates increased with an increase in the constant temperature Fig. 8. L. sericata completed larval development at 15°, 20° and 26°, but only managed partial development at a constant 10°, and most of the larvae died as 1st instars and the rest as early 2nd instars. This indicates that 10° is at the zero for development. It was recorded by Peairs (1927) that development did not occur, or did not continue to completion, at temperatures, in the constant temperature series, which approached to within one to five degrees of the zero point of the velocity curves. Observations of larvae showed that they would usually feed and grow to some extent, for a few days, at temperatures within one degree of the developmental zero. This appears to be the case in my observations with L. sericata.

The percentage of eggs hatching also dropped markedly at a constant 10° to about 50% as compared to over 90% at a constant 15°, 20° and 26°, although exact data for these were not recorded. Although there was only about a 50% hatch at 10°, most of the eggs contained full developed larvae. This was also recorded by Vogt and Woodburn (1980) when working with Lucilia cuprina eggs. They suggested that this failure to hatch may be associated with a lower level of larval activity at this temperature.

The experiment at 10° was started using 100 1st instar larvae, but I found a heavy mortality (96%), in the 1st instar and during the 1st - 2nd instar moult. The liver in the culture was changed after 12 days due to the bacterial infection of the liver from the dying larvae, but all the larvae were dead except for four 2nd instars after 18 days, so the experiment was stopped at this point. The

FIG 8. L. SERICATA LARVAL DEVELOPMENT AT A CONSTANT 15oC,20oC AND 26oC.

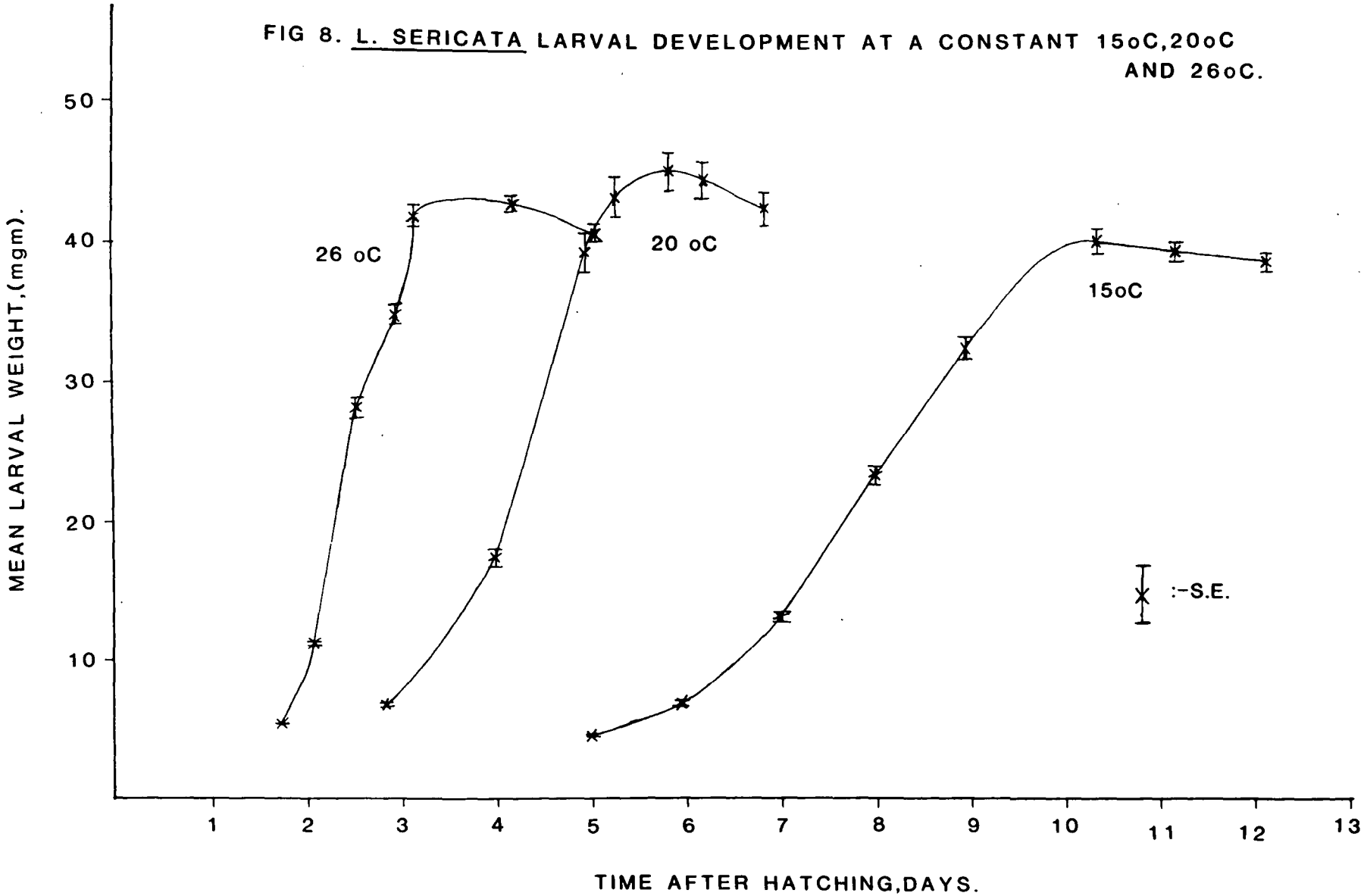


Table 14 Lucilia sericata, larval development as mean live weights (mgm) at constant 26°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
1.71	5.58	1.67	1.29	0.13	23.2	105
2.08	11.31	8.88	2.98	0.30	26.3	103
2.54	28.16	57.78	7.60	0.76	27.0	102
2.92	34.88	61.98	7.87	0.79	22.6	102
3.12	41.79	70.16	8.38	0.84	20.0	102
4.17	42.64	35.73	5.98	0.60	14.0	98
5.04	40.55	37.55	6.13	0.63	15.1	95

Table 15 Lucilia sericata, larval development as mean live weights (mgm) at constant 20°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
2.83	6.68	4.52	2.13	0.25	31.8	71
3.98	17.40	37.02	6.08	0.74	35.0	68
4.92	38.72	123.03	11.09	1.38	28.6	65
5.25	43.11	130.37	11.42	1.44	26.5	63
5.81	44.97	122.58	11.07	1.41	24.6	62
6.19	44.41	120.15	10.96	1.39	24.7	62
6.81	42.38	88.47	9.41	1.21	22.2	60

Table 16 *Lucilia sericata*, larval development as mean live weights (mgm) at constant 15°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
4.98	4.45	0.74	0.86	0.09	19.3	95
5.94	6.86	3.14	1.77	0.18	25.8	96
6.96	13.20	15.45	3.93	0.42	29.8	89
7.96	23.42	35.58	5.96	0.65	25.5	85
8.94	32.65	58.59	7.65	0.83	23.4	85
10.31	40.12	69.07	8.31	0.90	20.7	85
11.15	39.52	50.94	7.14	0.78	18.1	84
12.10	38.72	37.98	6.16	0.68	15.9	83

timings obtained from this experiment were Egg incubation at 102.25 hours and the duration of the 1st instar at 158 hours.

It can be seen from Tables 14, 15 and 16 that with L. sericata, as with C. vicina and C. vomitoria, the S.E. first of all increases as the mean larval weight increases. But unlike C. vicina and C. vomitoria where the S.E. decreases as the maximum mean weight is approached, in L. sericata the S.E. does not decrease until after the maximum mean weight has been achieved, Tables 14, 15 and 16. I would suggest that although this difference is significant, that it would have little effect on larval development as a whole, and would be best explained as a variation between different species.

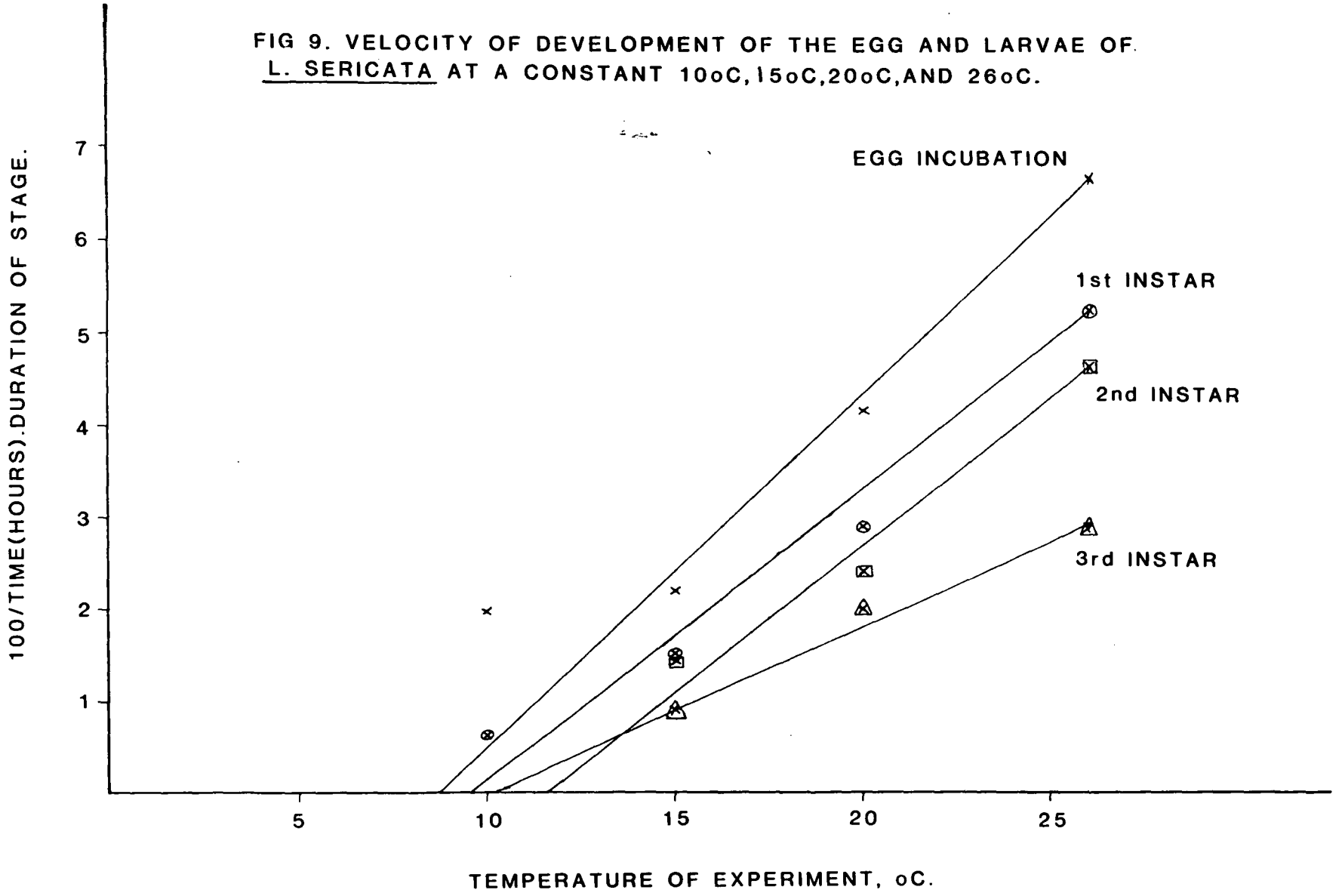
When a velocity graph is plotted, as used by Peairs (1927), a zero for development can be extrapolated. This is plotted for L. sericata in Fig. 9, where temperature is plotted against $\frac{100}{\text{time}}$ for each stage in hours, the lines being drawn in by eye.

Table 17 - Duration of egg and larval stages in the development of L. sericata, at the constant temperatures of 15°, 20° and 26°.

Constant temp.	Incubation time (hours)	Duration of 1st instar (hours)	Duration of 2nd instar (hours)	Duration of 3rd instar (hours)
15°	45.5	66.0	70.0	111.5
20°	24.0	34.5	41.5	50.0
26°	15.0	19.0	21.5	34.5

As can be seen from Fig. 9 the extrapolated zero, read from Fig. 9 is between about 8.7° and 11.5°, and a median zero temperature of 10.1° is used.

FIG 9. VELOCITY OF DEVELOPMENT OF THE EGG AND LARVAE OF L. SERICATA AT A CONSTANT 10oC, 15oC, 20oC, AND 26oC.



This zero temperature was then used to calculate the day-degrees required as before.

Table 18 - Day-degrees required by each stage, at the three constant temperatures, 15°, 20° and 26°, with L. sericata.

Temp. of experiment	Egg incubation	1st instar	2nd instar	3rd instar	(Total) complete development egg laying → max. mean weight
15°C	9.2	13.4	14.2	22.7	59.5
20°C	9.9	14.2	17.1	20.6	61.8
26°C	9.9	12.6	13.9	23.2	59.6

It can be seen from Table 18, that the 4 stages each have their own day-degree requirement, which is fairly constant for each of these stages. This means that the day-degree requirement determines the length of time each stage lasts, and hence the time for complete development, at these temperatures. This is a very similar result to that found with C. vomitoria, which also had thermal requirements for each of the stages, and a similar situation was recorded by Vogt and Woodburn (1980) on the eggs of Lucilia cuprina (Wiedemann), whose developmental rate increased linearly with temperature between 10° and 40° at constant saturation deficits.

The egg incubation times I recorded for L. sericata at 15°, 20° and 26°, Table 18 are very similar to those recorded by Davidson (1944) on L. sericata, who found a close correlation between the calculated and observed values from the velocity curve between 15° - 34.4°, which indicates a linear relationship between temperature and egg incubation over this temperature range. The egg incubation times are also similar to those recorded by Ash and Greenberg (1975) for L. sericata at 19° and 27°, but they also found that L. sericata egg and larval stages showed an inverse relationship to temperature

when the constant temperature was increased from 27° - 35°, which prolonged development. Hence 35° must be beyond the optimum temperature, and Cousin (1929) cited by Mackerras (1933) found 33° to be the optimum temperature for L. sericata larvae.

Individual live larval weight variations within each set of larvae of L. sericata, reared at the constant temperatures of 15°, 20° and 26°.

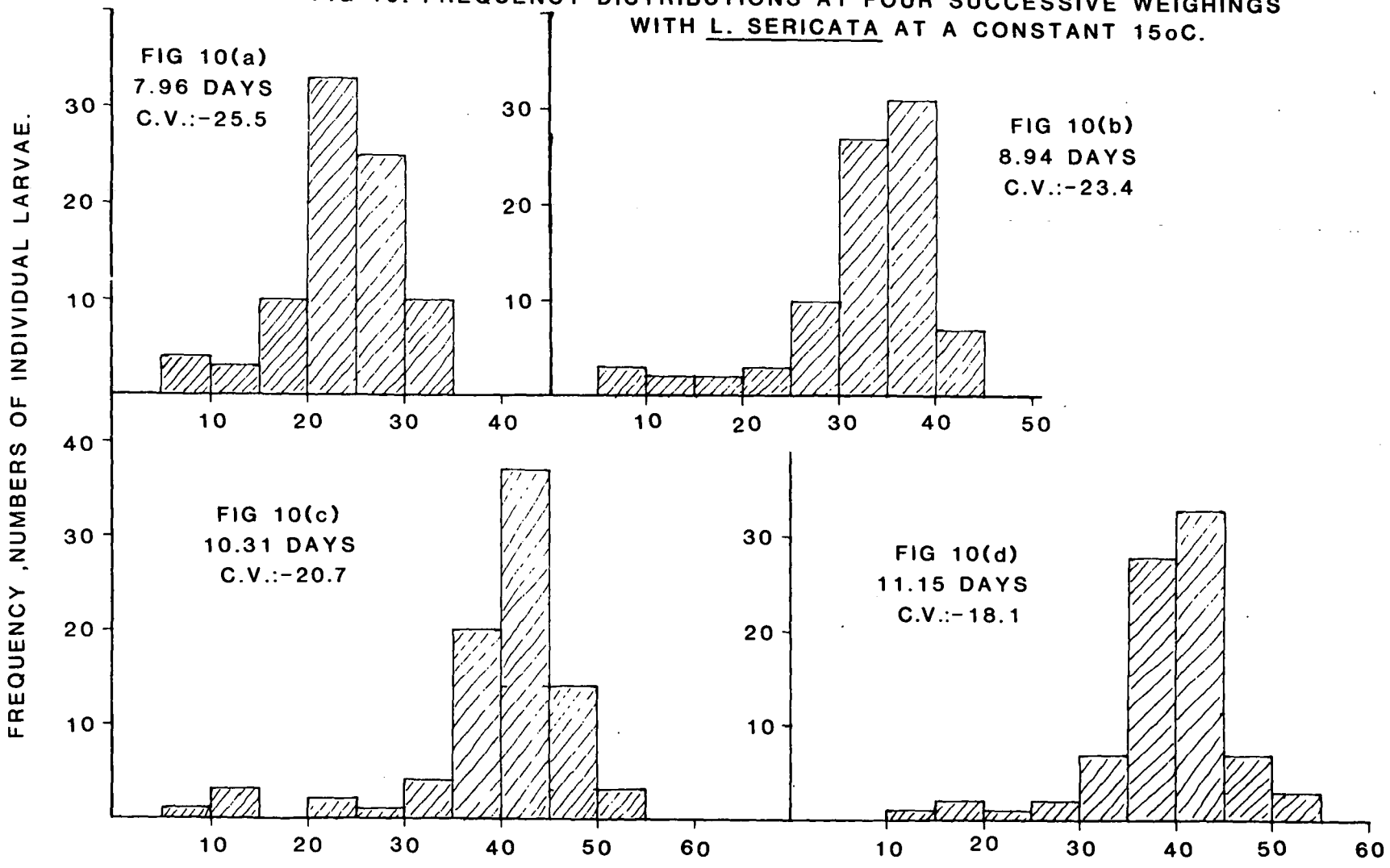
Looking at Fig. 10 a-d and Tables 14, 15 and 16, one can see that a rapidly increasing C.V. indicates that the larvae are entering into, or have entered into, a period of rapid growth, and that a decreasing C.V. indicates the end of a period of rapid growth, as described and found with C. vicina on Page 18.

When I calculated the range over which the C.V. was 75% of its maximum value, from Tables 14, 15 and 16, the following results were obtained, showing the mean larval weights between which rapid growth occurred at the three temperatures used.

15°	6.86 mg	-	32.65 mg
20°	6.68 mg	-	43.11 mg
26°	5.58 mg	-	34.88 mg

These results are quite different from those found from C. vicina, but very similar to those found for C. vomitoria, in that the rapid period of growth starts earlier, extends over a greater period of the larval development, and its timing is unaffected by different temperatures in L. sericata. This means that the rapid period of growth in this species starts around the mid-2nd instar and continues through until around maximum mean weight. In L. sericata the 1st - 2nd instar moult occurs at about a weight of 1.5 mg, and the 2nd - 3rd instar moult at about 8 mg.

FIG 10. FREQUENCY DISTRIBUTIONS AT FOUR SUCCESSIVE WEIGHINGS WITH L. SERICATA AT A CONSTANT 15oC.



Development of Phormia terrae-novae larvae at constant temperatures, 10°, 15°, 20° and 26°.

The developmental rates of P. terrae-novae showed similar temperature relationships as for the previous species, Fig. 11. P. terrae-novae completed larval development at 15°, 20° and 26°, but as in L. sericata managed only partial larval development at 10°, and most of the larvae died as mid-third instars, (Table 22). This indicates that 10° is close to, or at, the zero for development, atleast for the 3rd instar, in P. terrae-novae, as both the 1st and 2nd instars completed their development. This is to be expected, because as stated by Ash and Greenberg (1975), "as the physical and biochemical events that occur in the three stages of a holometabolous poikilotherm are so varied, it would be unrealistic to expect each stage to respond to a given temperature in the same way". So although in my calculations I have used the median zero for development from the velocity graph, each instar will have its own zero for development as shown on the velocity graph, but I decided to use the median value as it would give a more accurate overall extrapolated zero.

The fact that both L. sericata and P. terrae-novae both failed to complete larval development at 10°, whereas both C. vicina and C. vomitoria did complete development at this temperature, is in agreement with the findings of Cragg (1956) whose study included these four species, he found that the Calliphora species could withstand and develop at much lower temperatures than P. terrae-novae and L. sericata. He also noted that L. sericata had the highest mortality as he moved his experiments from 200 feet to 1850 feet above sea-level. This agrees with my study in that at 10° L. sericata died as 1st or early 2nd instars, whereas P. terrae-novae died as mid-third instars. So if the temperature was raised slightly up from 10°, P. terrae-novae

FIG 11. P.TERRAE-NOVAE LARVAL DEVELOPMENT AT A CONSTANT 15oC,20oC AND 26oC.

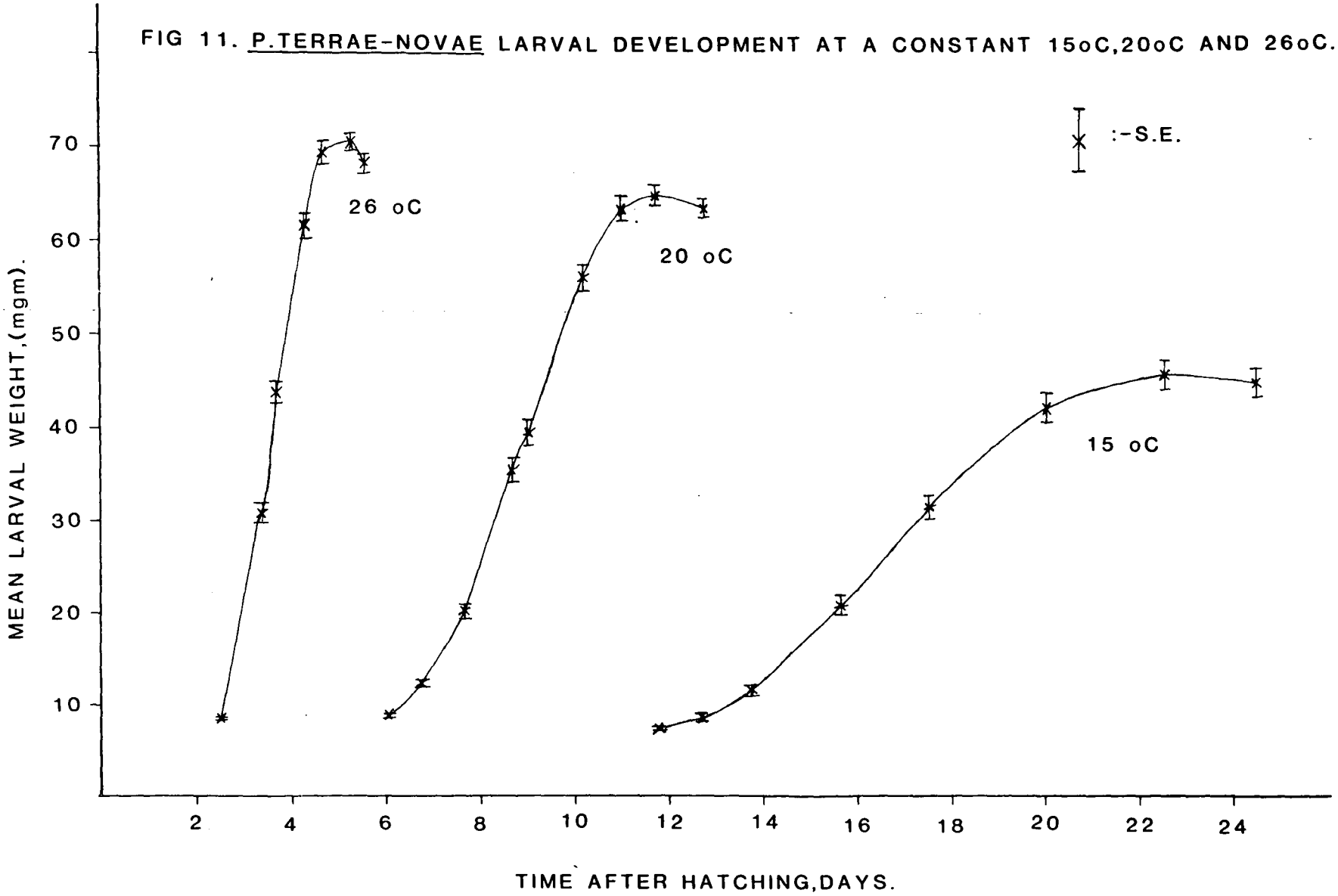


Table 19 *Phormia terrae-novae*, larval development as mean live weights (mgm) at constant 26°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
2.48	8.54	5.37	2.32	0.24	27.1	93
3.34	30.71	112.39	10.60	1.10	34.5	93
3.67	43.71	117.26	10.83	1.14	24.8	90
4.25	61.63	156.80	12.52	1.32	20.3	90
4.65	69.40	164.78	12.84	1.36	18.5	89
5.27	70.52	91.58	9.57	1.03	13.6	86
5.56	68.32	90.22	9.50	1.02	13.9	86

Table 20 *Phormia terrae-novae*, larval development as mean live weights (mgm) at constant 20°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
6.04	8.67	5.43	2.33	0.25	26.9	89
6.74	12.26	16.95	4.12	0.44	33.6	88
7.66	20.30	59.21	7.69	0.82	37.9	87
8.66	35.40	148.84	12.20	1.32	34.5	86
9.01	39.50	168.41	12.98	1.40	32.8	86
10.18	56.07	215.76	14.69	1.58	26.2	86
10.99	63.28	164.97	12.84	1.40	20.3	84
11.72	64.83	135.82	11.65	1.27	18.0	84
12.76	63.66	97.54	9.88	1.10	15.5	81

Table 21 *Phormia terrae-novae*, larval development as mean live weights (mgm) at constant 15°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
11.76	7.39	3.56	1.89	0.21	25.5	82
12.68	8.62	10.07	3.17	0.37	36.8	74
13.76	11.69	28.32	5.32	0.65	45.5	68
15.61	20.89	64.63	8.04	1.07	38.5	56
17.51	31.38	93.58	9.67	1.37	30.8	50
20.01	42.05	126.07	11.23	1.64	26.7	47
22.49	45.75	118.65	10.89	1.68	23.8	42
24.45	45.08	95.88	9.79	1.61	21.7	37

Table 22 *Phormia terrae-novae*, larval development as mean live weights (mgm) at constant 10°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	No. larvae
24.96	9.56	4.55	2.13	0.28	22.3	60
34.08	21.86	58.90	7.67	1.51	35.1	26
37.96	22.65	93.06	9.65	2.21	42.6	19
45.52	39.17	53.42	7.31	3.65	18.7	4

would have the better possibility of completing development.

It can be seen from Tables 19, 20 and 21 that with P. terrae-novae, as with C. vicina, C. vomitoria and L. sericata, the S.E. first of all increases as the mean larval weight increases. But unlike C. vicina and C. vomitoria, where the S.E. decreases as the maximum mean weight is approached, in P. terrae-novae, as with L. sericata, the S.E. does not decrease until after the maximum mean weight has been achieved, Tables 19, 20 and 21. I would suggest that, as with L. sericata, although the difference is significant, that it would have little effect on larval development as a whole, and would be best explained as a variation between different species.

When a velocity graph is plotted, as used by Peairs (1927), a zero for development can be extrapolated. This is plotted for P. terrae-novae in Fig. 12, where temperature is plotted against $\frac{100}{\text{time}}$ for each stage in hours, the lines being drawn in by eye.

Table 23 - Duration of egg and larval stages in the development of P. terrae-novae, at the constant temperatures of 15°, 20° and 26°.

Constant temperature	Incubation time (hours)	Duration of 1st instar (hours)	Duration of 2nd instar (hours)	Duration of 3rd instar (hours)
15°	60.25	129.0	147.75	203.5
20°	31.25	64.5	80.0	119.25
26°	18.5	38.5	19.5	53.5

As can be seen from Fig. 12, the extrapolated zero, read from Fig. 12, lies between 8.4° and 11.9°, and for further calculations a median zero temperature of 10.1° is used.

FIG 12. VELOCITY OF DEVELOPMENT OF THE EGG AND LARVAE OF P. TERRAE-NOVAE AT A CONSTANT 10oC,15oC,20oC AND 26oC.

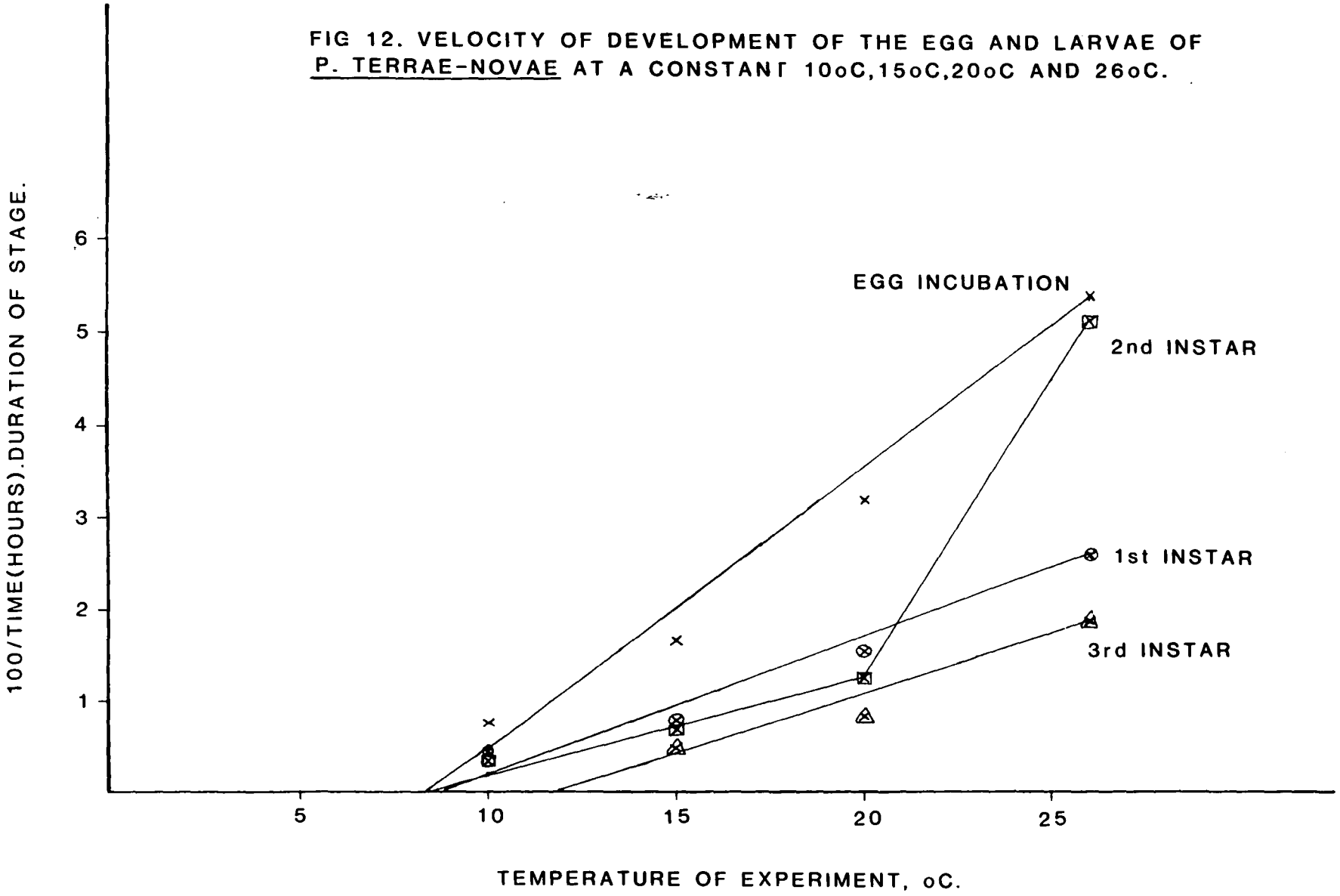


Table 24 - Day-degrees required by each stage, at the three constant temperatures 15°, 20° and 26°, with P. terrae-novae.

Temp. of experiment	Egg incubation	1st instar	2nd instar	3rd instar	(Total) complete development egg laying → max. mean weight
15°	12.2	26.2	30.0	41.3	109.7
20°	12.9	26.5	32.9	49.1	121.4
26°	12.2	25.5	12.9	35.4	86.0

It can be seen from Table 24 that egg incubation and 1st instars both have their own thermal requirement in day-degrees for their development, which is constant for both of these stages at the temperatures used in these experiments. Whereas the durations of the 2nd and 3rd instars are not dependent on the day-degree requirement alone. I suggest the following explanations for these results.

1. Experimental error. This is extremely unlikely as the timings in these experiments for the 2nd instar at 15° would have to have been some 2.5 days out, and about 1.75 days at 20°.

2. a) Relatively slower development at the lower temperatures in day-degrees, by stimulation by high temperatures and or inhibition by lower temperatures.

b) Adaptation by P. terrae-novae to develop faster at higher temperatures. Since P. terrae-novae is a myiasis causing species it is not unreasonable to suspect that it would be able and adapted to develop relatively quicker at around body temperature, i.e. about 30° to 35°. The explanation for the thermal requirement of the egg incubation and 1st instar is that these are present in the fur or on the skin of the victim, i.e. exposed, and will be adapted to develop at lower temperatures than the 2nd and 3rd instars, which will perhaps burrow into the victim and be adapted to developing at higher temperatures.

Individual live larval weight variations within each set of larvae of P. terrae-novae, reared at the constant temperatures of 15°, 20° and 26°.

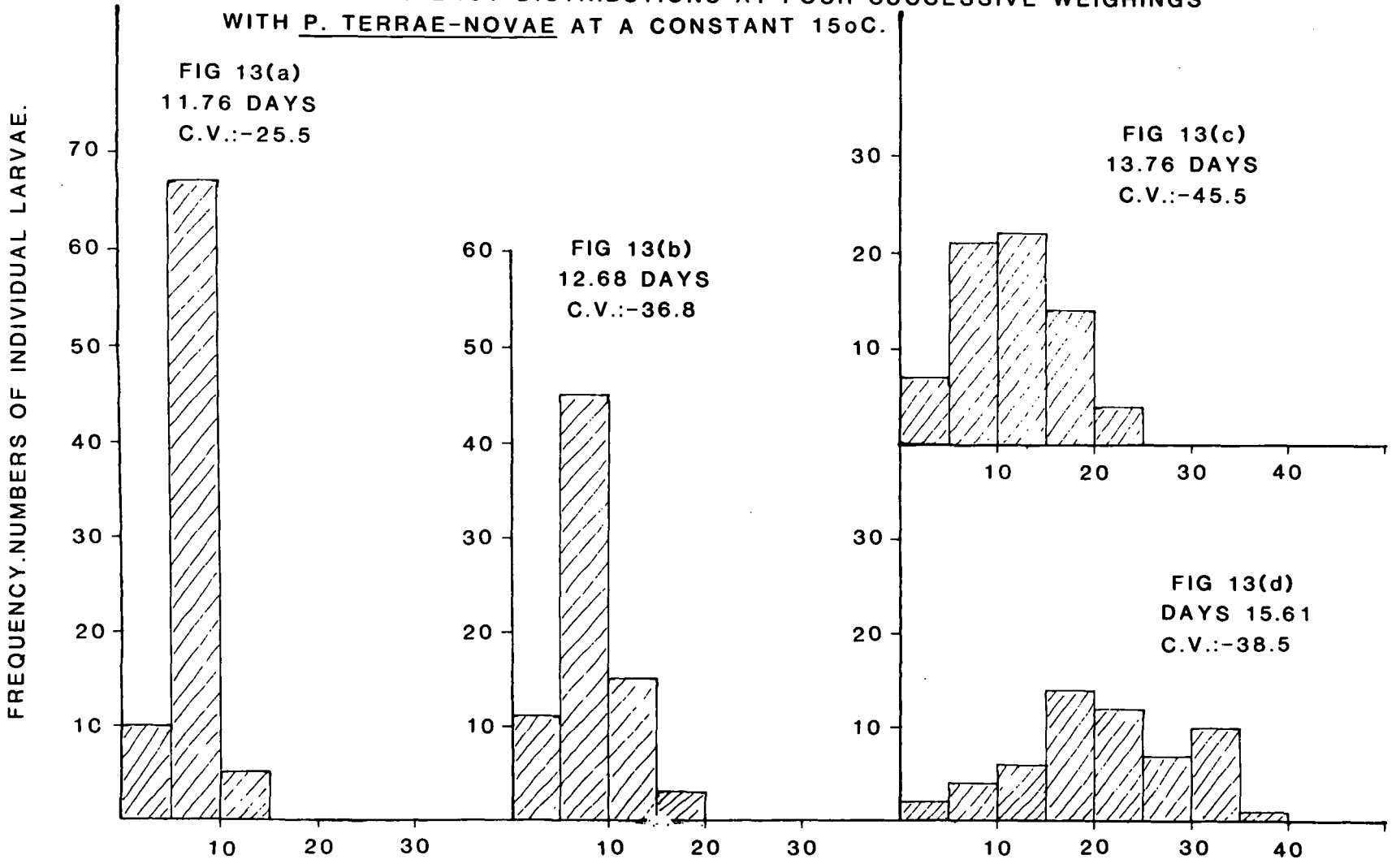
Looking at Fig. 13 a-d and Tables 19, 20 and 21 can see that a rapidly increasing C.V. indicates that the larvae are entering into, or have entered into, a period of rapid growth, and that a decreasing C.V. indicates the end of a period of rapid growth, as described and found with C. vicina on Page 18.

When I calculated the range over which the C.V. was 75% of its maximum value, from Tables 19, 20 and 21, the following results were obtained, showing the mean larval weights between which rapid growth occurred at the three temperatures used.

15°	8.62 mg	-	20.89 mg
20°	12.26 mg	-	39.5 mg
26°	8.54 mg	-	30.71 mg

The period of rapid growth in P. terrae-novae starts around the end of the 2nd instar and continues through until around the mid-3rd instar, and its timing, as found with C. vomitoria on Page 24, appears to be unaffected by the prevailing constant temperature, within the range of temperatures used in these experiments. In P. terrae-novae the 1st - 2nd instar moult occurring at about 1.5 mg, and the 2nd - 3rd instar moult at about 8.5 mg.

FIG 13. FREQUENCY DISTRIBUTIONS AT FOUR SUCCESSIVE WEIGHINGS WITH P. TERRAE-NOVAE AT A CONSTANT 15oC.



Calliphora vicina larvae reared under conditions of alternating temperatures.

The larvae of C. vicina were reared under conditions of alternating temperatures, 5° - 15°, 10° - 20° and 15° - 26°, as described on page 8. The results from these three experiments are set out in Tables 25, 26 and 27 and Fig. 14.

The duration of egg incubation, and the three instars up to maximum mean weight were noted at each of the two temperatures in each experiment (Table 28, page 35f), the method for determining egg incubation is the same as used for the constant temperature series as described on page 5 and the larval moults as described on page 7.

I then calculated the day-degree requirement for each of these stages under the three different conditions of alternating temperatures, using the calculated zero for development of 4.8° from the constant temperature experiments (see pages 12 and 13). These results were then compared to those from the constant temperature series on Table 29.

Table 29 - Calliphora vicina, a comparison of the day-degree requirements of eggs and larvae up to maximum mean weight at constant and alternating temperatures.

	10°	5°-15°	15°	10°-20°	20°	15°-26°
Egg incubation	15.9	14.0	15.3	15.0	16.0	16.6
1st instar	15.3	14.3	13.7	14.3	14.1	14.8
2nd instar	19.4	30.8	17.2	20.1	20.1	19.0
3rd instar	21.8	47.6	26.8	57.3	43.7	55.5
Total	72.4	96.7	73.0	106.7	93.9	105.9

FIG 14. C. VICINA, LARVAL DEVELOPMENT UNDER CONDITIONS OF ALTERNATING TEMPERATURES BETWEEN 5oC-15oC, 10oC-20oC AND 15oC-26oC.

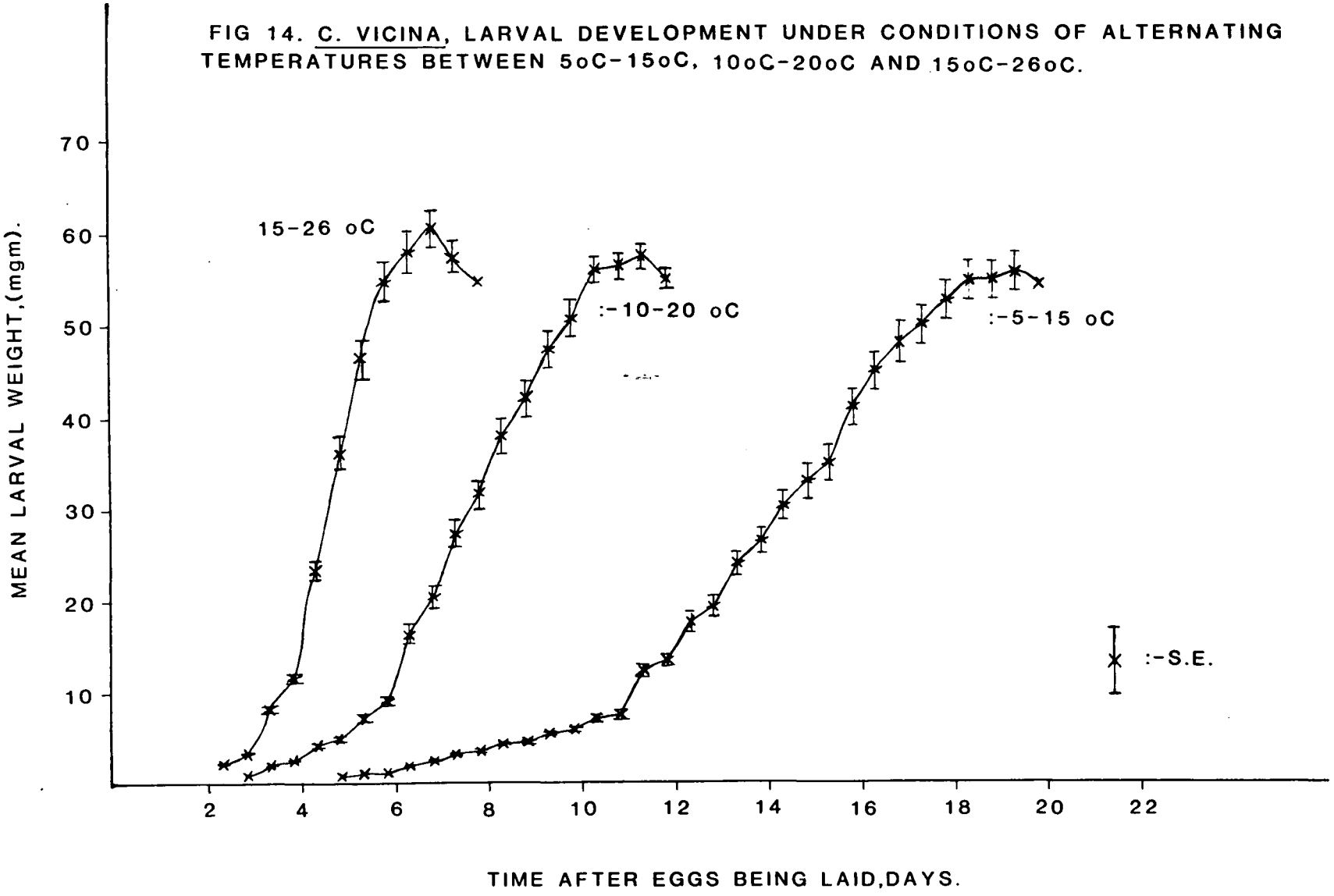


Table 25 Calliphora vicina, larval development as mean live weights (mgm) under conditions of alternating temperatures between 15°C - 26°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
2.31	2.08	0.40	0.63	0.07	30.5	15°C	74
2.81	3.30	0.95	0.97	0.12	29.5	26°C	70
3.31	8.03	6.97	2.64	0.37	32.9	15°C	51
3.81	11.61	18.27	4.27	0.59	36.8	26°C	52
4.31	23.39	66.46	8.15	1.13	34.8	15°C	52
4.81	36.03	164.72	12.83	1.80	35.6	26°C	51
5.31	46.61	228.31	15.11	2.14	32.4	15°C	50
5.81	54.70	265.02	16.28	2.30	29.8	26°C	50
6.31	57.93	269.46	16.42	2.32	28.3	15°C	50
6.81	60.78	207.28	14.40	2.08	23.7	26°C	48
7.31	57.30	168.92	13.00	1.88	22.7	15°C	48
7.81	54.91	-	-	-	-		48

Table 26 *Calliphora vicina*, larval development as mean live weights (mgm) under conditions of alternating temperatures between 10°C - 20°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. Larvae
2.81	0.91	-	-	-	-		81
						20°C	
3.31	1.93	0.22	0.47	0.05	24.5		77
						10°C	
3.81	2.39	0.50	0.70	0.08	29.4		74
						20°C	
4.31	4.00	1.89	1.38	0.17	34.4		65
						10°C	
4.81	4.94	2.79	1.67	0.21	33.8		64
						20°C	
5.31	7.02	8.98	3.00	0.37	42.7		65
						10°C	
5.81	9.06	18.04	4.25	0.55	46.9		59
						20°C	
6.31	16.32	55.15	7.43	1.00	45.5		55
						10°C	
6.81	20.51	80.36	8.96	1.20	43.7		56
						20°C	
7.31	27.35	123.49	11.11	1.53	40.6		53
						10°C	
7.81	31.87	157.39	12.55	1.72	39.4		53
						20°C	
8.31	38.07	202.53	14.23	1.95	37.4		53
						10°C	
8.81	42.22	211.63	14.55	2.04	34.5		51
						20°C	
9.31	47.57	209.57	14.48	2.03	30.4		51
						10°C	
9.81	50.92	205.97	14.35	2.05	28.2		49
						20°C	
10.31	56.11	103.62	10.18	1.53	18.1		44
						10°C	
10.81	56.79	83.39	9.13	1.38	16.1		44
						20°C	
11.31	57.80	78.35	8.85	1.33	15.3		44
						10°C	
11.81	55.11	66.16	8.13	1.23	14.8		44

Table 27 Calliphora vicina, larval development as mean live weights (mgm) under conditions of alternating temperatures between 5°C - 15°C

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
4.81	0.76	-	-	-	-		118
						15°C	
5.31	1.00	-	-	-	-		108
						5°C	
5.81	1.10	-	-	-	-		106
						15°C	
6.31	1.92	0.24	0.49	0.05	25.8		87
						5°C	
6.81	2.34	0.43	0.65	0.08	27.9		72
						15°C	
7.31	3.09	0.86	0.93	0.11	30.1		73
						5°C	
7.81	3.58	1.16	1.08	0.13	30.1		71
						15°C	
8.31	4.28	1.53	1.24	0.15	28.8		64
						5°C	
8.81	4.46	1.67	1.29	0.17	29.0		59
						15°C	
9.31	5.65	2.26	1.50	0.20	26.6		56
						5°C	
9.81	5.93	3.04	1.74	0.23	29.4		55
						15°C	
10.31	8.14	10.20	3.19	0.45	39.2		51
						5°C	
10.81	8.47	12.22	3.50	0.48	41.3		52
						15°C	
11.31	12.50	19.89	4.46	0.64	35.7		48
						5°C	
11.81	13.41	23.59	4.86	0.71	36.2		47
						15°C	
12.31	17.72	49.97	7.07	1.02	39.9		48
						5°C	
12.81	19.27	60.24	7.76	1.12	40.3		48
						15°C	
13.31	24.10	102.99	10.15	1.46	42.1		48
						5°C	
13.81	26.76	113.51	10.65	1.55	39.8		47
						15°C	
14.31	30.57	147.61	12.15	1.77	39.7		47
						5°C	
14.81	33.23	167.97	12.96	1.89	39.0		47
						15°C	
15.31	35.16	179.31	13.39	1.95	38.1		47
						5°C	
15.81	41.26	174.50	13.21	1.97	32.0		45

Table 27 (Contd.)

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
						15°C	
16.31	45.23	184.77	13.59	2.03	30.0		45
						5°C	
16.81	48.20	200.81	14.17	2.14	29.4		44
						15°C	
17.31	50.21	214.92	14.66	2.21	29.2		44
						5°C	
17.81	52.98	205.30	14.33	2.16	27.0		44
						15°C	
18.31	55.06	214.49	14.65	2.21	26.6		44
						5°C	
18.81	55.20	195.88	14.00	2.11	25.3		44
						15°C	
19.31	55.98	196.75	14.03	2.11	25.1		44
						5°C	
19.81	54.70	-	-	-	-		44

Table 28 C. vicina, durations of egg and larval stages under different conditions of alternating temperatures.

Alternating temperatures of experiment	Time of egg laying, (placed at higher of two temps.).	Egg Incubation, time at each temperature.	Ist Instar, time at each temperature.	2nd Instar, time at each temperature.	3rd Instar until maximum mean weight, time at each temperature.
15° - 26°	1.30 p.m.	13 hrs. at 26° plus 12 hrs. at 15°	11 hrs. at 26° plus 12 hrs. at 15°	15.75 hrs. at 26° plus 12 hrs. at 15°	39.75 hrs. at 26° plus 48 hrs. at 15°
10° - 20°	1.30 p.m.	19.5 hrs. at 20° plus 12.25 hrs. at 10°	14.5 hrs. at 20° plus 23.75 hrs. at 10°	23.5 hrs. at 20° plus 24 hrs. at 10°	70 hrs. at 20° plus 60 hrs. at 10°
5° - 15°	1.30 p.m.	32.25 hrs. at 15° plus 36 hrs. at 5°	33.25 hrs. at 15° plus 24 hrs. at 5°	48 hrs. at 15° plus 48 hrs. at 5°	110 hrs. at 15° plus 120 hrs. at 5°

It can be seen from Table 29, that in C. vicina there is a thermal requirement in day-degrees, which remains fairly constant, for egg incubation, 1st and 2nd instars at both constant and alternating temperatures over the range of 5° - 26°. However the 3rd instar to maximum mean weight has a higher thermal requirement under alternating temperatures as compared to that of constant temperatures, and as noted previously, the lower the constant temperature the less the thermal requirement in the 3rd instar.

This shows that there is approximately a linear relationship with temperature, both constant and alternating, between 5° and 26° in egg incubation, 1st and 2nd instar development. However the duration of the 3rd instar to maximum mean weight is much longer at alternating than one would expect from the results of the constant temperature series. These results from C. vicina therefore agree with those of Hanski (1977) working on L. illustris. He found that the observed production rate at changing temperatures, which was measured by the increase in fresh weight between successive weighings, was lower than the prediction from the constant temperature experiments. He concluded that net production efficiency was lower at changing than at constant temperatures, atleast in the 3rd instar larvae in L. illustris. He further suggests that when the larvae are at the stage of the highest production rate, their metabolism is possibly channelled to the synthesis of new tissue to such an extent that they are less "efficiently buffered" against enviromental stress, such as suboptimal temperature conditions, which he states on the other hand, may be interpreted as an adaptation to maximize the utilization of suitable conditions.

The above is a good example of how different stages in development are sensitive to different regimes. Meyer and Schaub (1973) on Callitroga macellaria, Lucilia cuprina and Calliphora vicina, found that within fixed limits of tolerance, the reaction to changes in temperature

is more intensive in feeding than in non-feeding larvae, and that a high metabolic rate is related to high levels of sensitivity to temperature changes.

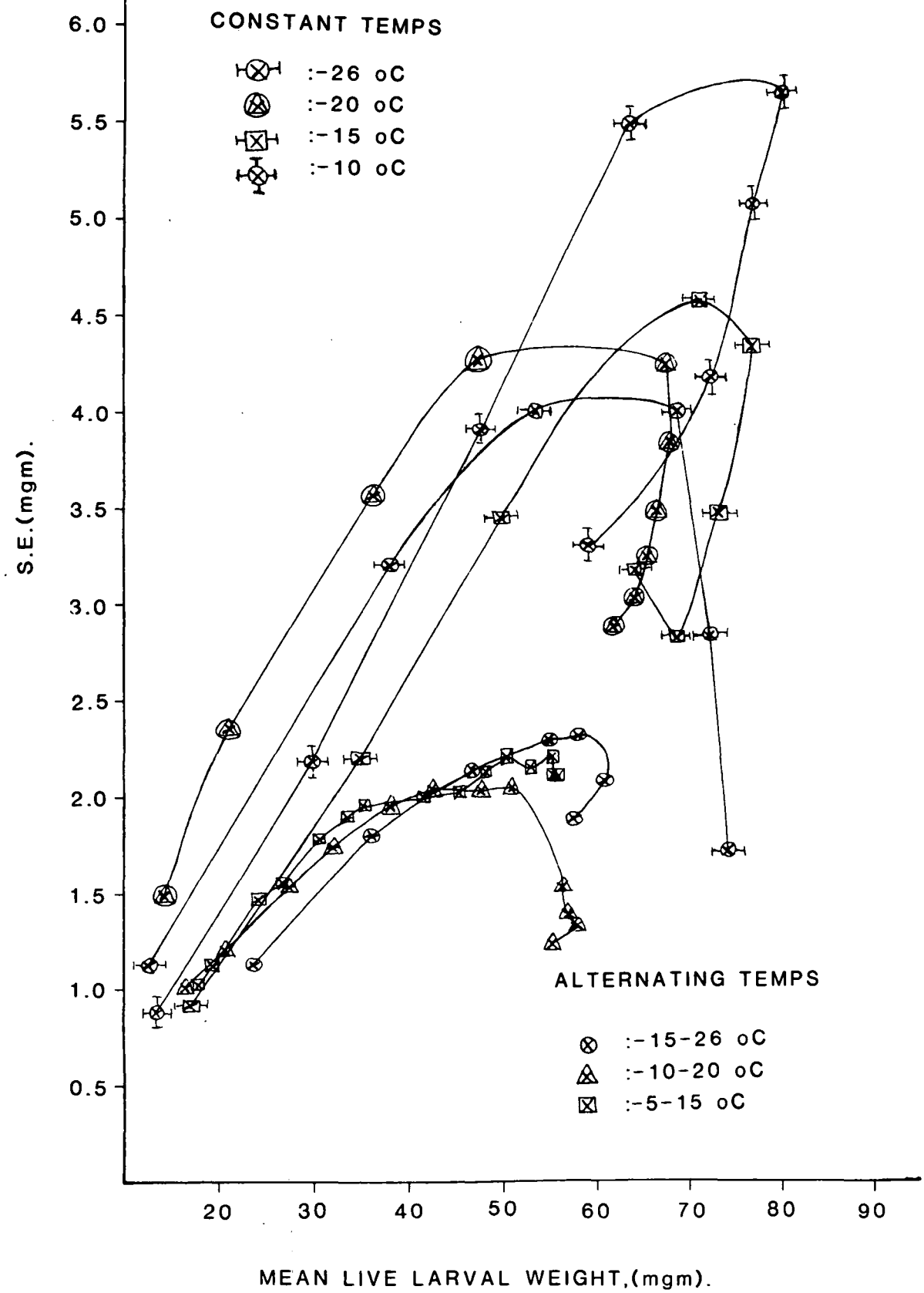
This effect on the 3rd instar of C. vicina of temperature alternation could well be affecting the enzymatic system of the larva. Grosse (1976) found that during the 3rd instar of C. vicina the glycogen level in the fat body increases continuously, and that the activity of glycogen phosphorylase a in the fat body increases by some 300% over the 3rd instar and pre-pupa stage then falls dramatically at the end of the pre-pupa stage.

It is best summed up by Ash and Greenberg (1975), that as the physical and biochemical events that occur in the 3 stages of a holometabolous poikilotherm are so varied, that it would be unrealistic to expect each stage to respond to a given temperature in the same way.

Not only do alternating temperatures effect the duration of the 3rd instar but also effect the individual weight heterogeneity within each batch, in the 3rd instar (Fig. 15, page 37a) which is shown by the large differences in the S.E. between constant and alternating temperatures. C. vicina moults from 1st - 2nd instar at about 1 - 1.5 mg and from 2nd - 3rd instar at about 6 - 9 mg. At these points the S.E., comparing constant and alternating temperatures, are very similar expecially when the lower constant temperatures are used for the comparison. At early 3rd instar, around a weight of 15 mg, the higher constant temperatures promote this difference, whereas at late 3rd instar (50 mg plus) the lower constant temperatures having the greater affect; i.e. at a mean weight of 20 mg the S.E. at 20° was 2.22 mg, at 10° was 1.425 mg and at the alternation 15° - 26° was 1.00 mg, whereas at a mean weight of 60 mg at 20° was 4.35 mg, at 10° was 5.2 mg and at the alternation 15° - 26° was 2.25 mg.

Under conditions of alternating temperatures the S.E. appears to

FIG 15. C. VICINA PLOT OF S.E. V MEAN LIVE LARVAL WEIGHT AT BOTH CONSTANT AND ALTERNATING TEMPERATURES



Note: Successive points in time have been joined up.

be independent of the prevailing temperatures (Fig. 15).

It can be suggested that this difference between constant and alternating temperatures is brought about by the alternation of temperature affecting the rate of food ingestion or digestion (assimilation) or both. The crops of the larvae under alternating temperature conditions did not appear to be less full than those of larvae reared under constant temperature conditions, from which comes the suggestion that the fluctuation in temperature, (large i.e. 10^{o}), is effecting the efficiency of the gut enzymes in the rate of digestion of the food, or in the uptake/assimilation of the digested food.

Watt (1968) cited by Hanski (1977) considers that we ought to be able to understand the effects of temperature fluctuations "by summing the effects of each of the temperatures experienced, as each of the effects would be predicted from a curve for the effect of constant temperature." From the above results I would argue that in nature, not only are the temperatures of great importance, but also the change in temperatures, as the animals tolerance to a change in temperature varies depending on the conditions in which it has been kept.

So the alternating temperatures not only affect the time required for varying stages of the life-cycle of the larvae, but also the weight heterogeneity within a population. This lower and more uniform S.E. at alternating temperatures compared to constant temperatures, shows a much lower weight variation between individuals of a given batch. As mentioned previously, changes in temperature, i.e. alternating temperatures, will be expected to have their greatest affect during periods of intensive growth, such as the 3rd instar larvae. This reduction in intensive growth by alternation of temperature seems to reduce the S.E. found within a population of larvae. This effect is more than likely at an enzymatic level, and further work is

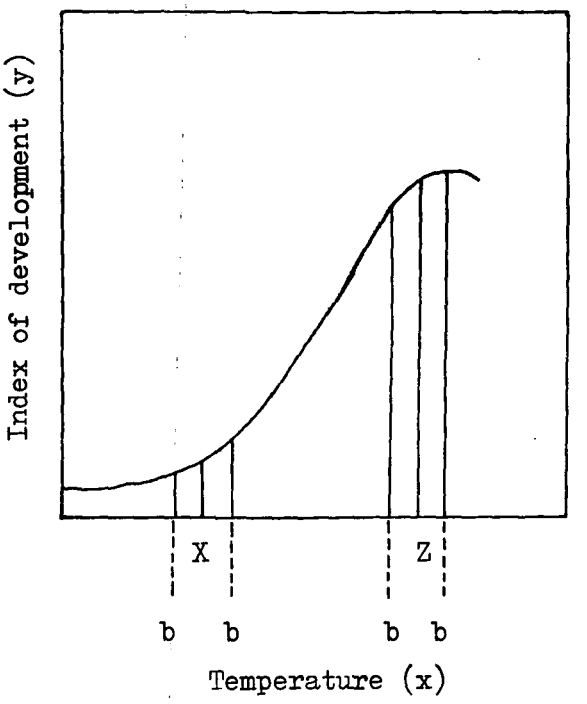
required to elucidate more precisely the effect of alternating temperatures.

Most of the workers investigating the relationship between temperature and insect development have made use of constant temperatures maintained by various devices within incubators, so much so that it has become a serious problem as to how far the results obtained under constant temperatures of the incubators can be taken to be applicable to the fluctuating temperatures prevalent in the field. Some workers in the past (Shelford (1927) on the codlingmoth Carpocapsa pomonella and Peairs (1927) on various Lepidoptera, Diptera and Coeloptera) have noted that variable temperatures bring about some acceleration in insect development. Headlee (1940) investigated this problem more critically by maintaining fluctuating and constant temperatures in parallel experiments, but he found acceleration in some series and retardation in others. In trying to explain these apparently discordant results he said that as the characteristic curve of reaction of insects to external factors of the environment happens to be sigmoid, the speed of metabolism is likely to be reduced, and more time required to complete the same metabolic changes in the variable, than would be necessary to complete the same changes in the constant, if the variable range under examination goes over into the 'foot' part of the curve or into the top or steeper part of the curve.

Pradhan (1944) on the cotton bollworm pupae drew a graph of pupal period versus temperature using a good number of temperature averages extending over the full range of seasonal fluctuation. When Pradhan compared this with the curve obtained under constant temperature by Ahmad and Ghulam Ullah (1939) a very instructive result was indicated, because the curve obtained under fluctuating temperature started much lower, (starting from lower temperature), than that obtained under constant temperature, and then gradually approaching it and

actually tends to cross it and go above it at higher temperatures. This comparison tends to indicate that the development is quicker under variable temperatures than under constant temperatures at lower temperatures, but the effects are just reversed at higher temperatures, when development is slower under variable temperatures than under constant temperatures. This was explained by Pradhan by the following method:-

Taking the curve of developmental indices or reciprocal $\left(\frac{1}{\text{developmental time}}\right)$ to be sigmoid in shape i.e. a curve with two opposite bends and a point of inflection in between, the effect of variable temperatures can be explained as follows:-



Curve of Developmental Indices.

Suppose the average of fluctuating temperature is x in the lower bend of the curve. Now it is clear that in the case of the temperature remaining constantly at x then the rate of development will remain constant, but in the case of fluctuating temperature, the development will be quicker when the temperature goes above x, i.e. the effect will be retardative as compared to the constant temperature at x; and the resultant effect of the fluctuating temperature will be the sum of these accelerative and retardative effects. Then as the graph in the region of the lower bend is bent upwards the rate of retardation below x is slower than acceleration above x, so the resultant effect of variable temperature is accelerative. The effects around z will be opposite and therefore in aggregate retardative.

During my experiments with C. vicina larvae, I found no accelerative or retardative effects with alternating temperatures compared to constant temperatures, over the temperature range used in these experiments, during egg incubation, 1st and 2nd instars. However in the 3rd instar I found a retardative effect in terms of day-degrees required (Table 29) throughout the temperature range with alternating temperatures.

Therefore I would argue that Pradhan's explanation, however logical, is an over simplification, and he does not take into account the animals reaction to a large change in temperature. The animal might survive well at both 5° and 30°, but what sort of thermal shock would the animal undergo if it is changed quickly from one temperature to the other? Neither does Pradhan take into account that the animal will react differently to temperature and temperature changes at different stages in its development. I would suggest that it is dangerous to reduce an animals reaction to factors such as temperature into mathematical formulae, as we are presuming that we have taken all factors into account, and this will often lead to incorrect deductions.

Calliphora vomitoria larvae reared under conditions of alternating temperatures.

The larvae of C. vomitoria were reared under conditions of alternating temperatures, 10° - 20° and 15° - 26°, as described on page 8 of this thesis. The results from these experiments are set out on Tables 30 and 31, and Fig. 16, (pages 42a-c, following this page).

The duration of egg incubation, 1st instar, 2nd instar and the 3rd instar up to maximum mean weight were noted at each of the two temperatures used in each experiment, Table 32. The method for determining egg incubation and the larval moults is the same as used for the constant temperature series as described on pages 5 and 7 respectively.

I then calculated the day-degree requirement for each of these stages under the different conditions of alternating temperatures, using the calculated zero for development of 5.7° from the constant temperature experiments, see page 21. These results were then compared to those from the constant temperature series on Table 33

Table 33 - Calliphora vomitoria, a comparison of the day-degree requirement of eggs and larvae up to maximum mean weight at constant and alternating temperatures.

	15°	10°-20°	20°	15°-26°
Egg incubation	17.9	14.1	14.5	14.4
1st instar	24.4	20.4	22.7	21.8
2nd instar	25.0	24.0	28.3	21.0
3rd instar	50.4	29.7	48.3	52.9
Total	117.7	88.2	113.8	110.1

FIG 16. C. VOMITORIA, LARVAL DEVELOPMENT UNDER CONDITIONS OF ALTERNATING TEMPERATURES BETWEEN 10oC-20oC AND 15oC-26oC.

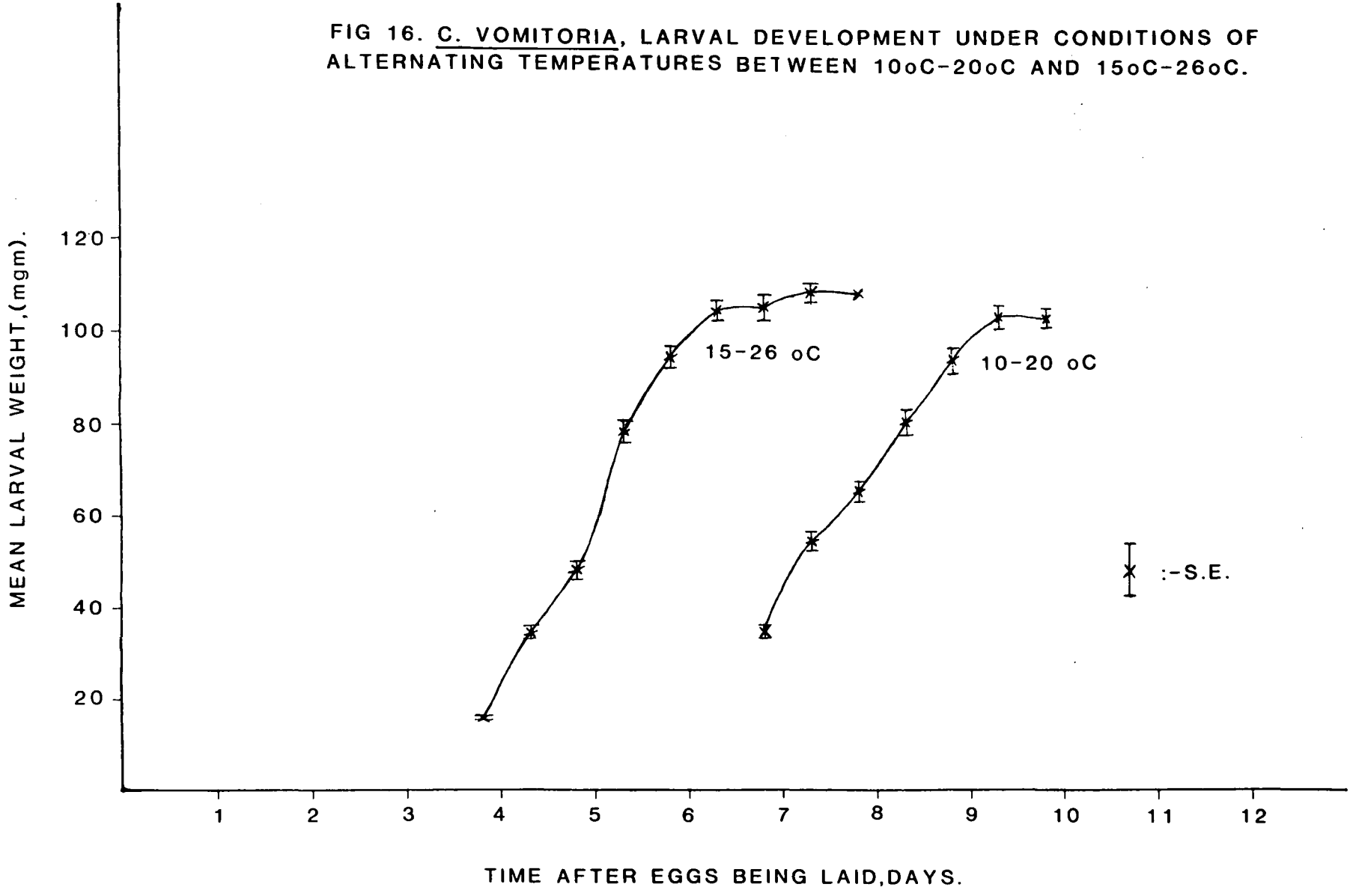


Table 30 *Calliphora vomitoria*, larval development as mean live weights (mgm) under conditions of alternating temperatures between 15°C - 26°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
3.81	15.37	18.11	4.26	0.43	27.7	15°C	96
4.31	34.78	173.62	13.18	1.45	37.9	26°C	83
4.81	48.45	340.83	18.46	2.05	38.1	15°C	81
5.31	78.19	462.23	21.50	2.43	27.5	26°C	78
5.81	94.15	489.95	22.13	2.54	23.5	15°C	76
6.31	104.34	464.89	21.56	2.46	20.7	26°C	77
6.81	104.99	587.57	24.24	2.74	23.1	15°C	77
7.31	108.49	342.87	18.52	2.12	17.1	26°C	76
7.81	108.19	-	-	-	-	15°C	74

Table 31 Calliphora vomitoria, larval development as mean live weights (mgm) under conditions of alternating temperatures between 10°C - 20°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
						10°C	
6.81	34.60	138.90	11.79	1.40	34.1	20°C	71
7.31	54.55	304.25	17.44	2.10	32.0	10°C	69
7.81	65.04	469.18	21.66	2.59	33.3	20°C	70
8.31	80.65	699.24	26.44	3.16	32.8	10°C	70
8.81	93.43	625.60	25.01	3.01	26.8	20°C	69
9.31	103.14	430.35	20.74	2.52	20.1	10°C	68
9.81	102.85	359.59	18.96	2.30	18.4		68

Table 32 *C. vomitoria*, duration of egg and larval stages

under different conditions of alternating temperatures.

Alternating temperatures of experiment	Time of egg laying, (placed at higher of two temps.).	Egg Incubation, time at each temperature.	Ist Instar, time at each temperature.	2nd Instar, time at each temperature.	3rd Instar until maximum mean weight, time at each temperature.
15° - 26°	1.30 p.m.	11.5 hrs. at 26° plus 12 hrs. at 15°	20 hrs. at 26° plus 12.5 hrs. at 15°	14 hrs. at 26° plus 23.5 hrs. at 15°	46 hrs. at 26° plus 36 hrs. at 15°
10° - 20°	1.30 p.m.	19.5 hrs. at 20° plus 14 hrs. at 10°	24 hrs. at 20° plus 34 hrs. at 10°	33 hrs. at 20° plus 24 hrs. at 10°	39 hrs. at 20° plus 36 hrs. at 10°

It can be seen from Table 33, that when you compare the alternation of temperature 15° - 26° with a constant 20°, that both egg incubation and the 1st instar have a thermal requirement which remains fairly constant. However, the 2nd instar appears to develop quicker at the alternating temperature 15° - 26°. This could be an example of how different stages react to temperature in different ways, but further investigation is required before a definite statement could be made. However these differences occur, the overall total thermal requirement remains about the same at 15° - 26° alternation as at a constant 20°.

When comparing the alternation of temperature 10° - 20° with a constant 15°, it is found that an alternation of temperature lowers the thermal requirement, and hence increases the rate of development, to varying degrees, in all of the larval stages and egg incubation, but especially it increases the rate of development of the 3rd instar. So the overall total thermal requirement is much less at the alternating temperature 10° - 20° than at a constant 15° (Table 33).

This finding that an alternation of temperature, at the lower temperatures (10° - 20°), increases the rate of develpment of C. vomitoria, and most notably in the 3rd instar, is opposite to the case I found with C. vicina where the effect of alternating temperatures (also 10°C - 20°C) was retardative in the 3rd instar. This increased developmental rate in C. vomitoria is also the opposite to the findings of Hanski (1977) with Lucilia illustris, who concluded that the net production efficiency was lower at changing than at constant temperatures, at least in the 3rd instar larvae.

My findings show that in C. vomitoria this effect can be reversed, and alternating temperatures increasing net production efficiency, and thus speed of development, compared to constant temperatures. The effect of alternating temperatures being accelerative on developmental rate was also found by Shelford (1927) on the codlingmoth

Carpocapsa pomonella and by Pearis (1927) on various Lepidoptera, Diptera (including C. vomitoria pupae), and Coleoptera.

The findings of Meyer and Schaub (1973) on Callitroga macellaria, Lucilia cuprina and Calliphora vicina, which I used to explain the retardative effect of alternating temperatures with C. vicina hold true for the effect being accelerative with C. vomitoria, because they found that within fixed limits of tolerance, the reaction to changes in temperature is more intensive in feeding than in non-feeding larvae, hence this reaction could be either accelerative or retardative during the intensive feeding of the 3rd instar larvae.

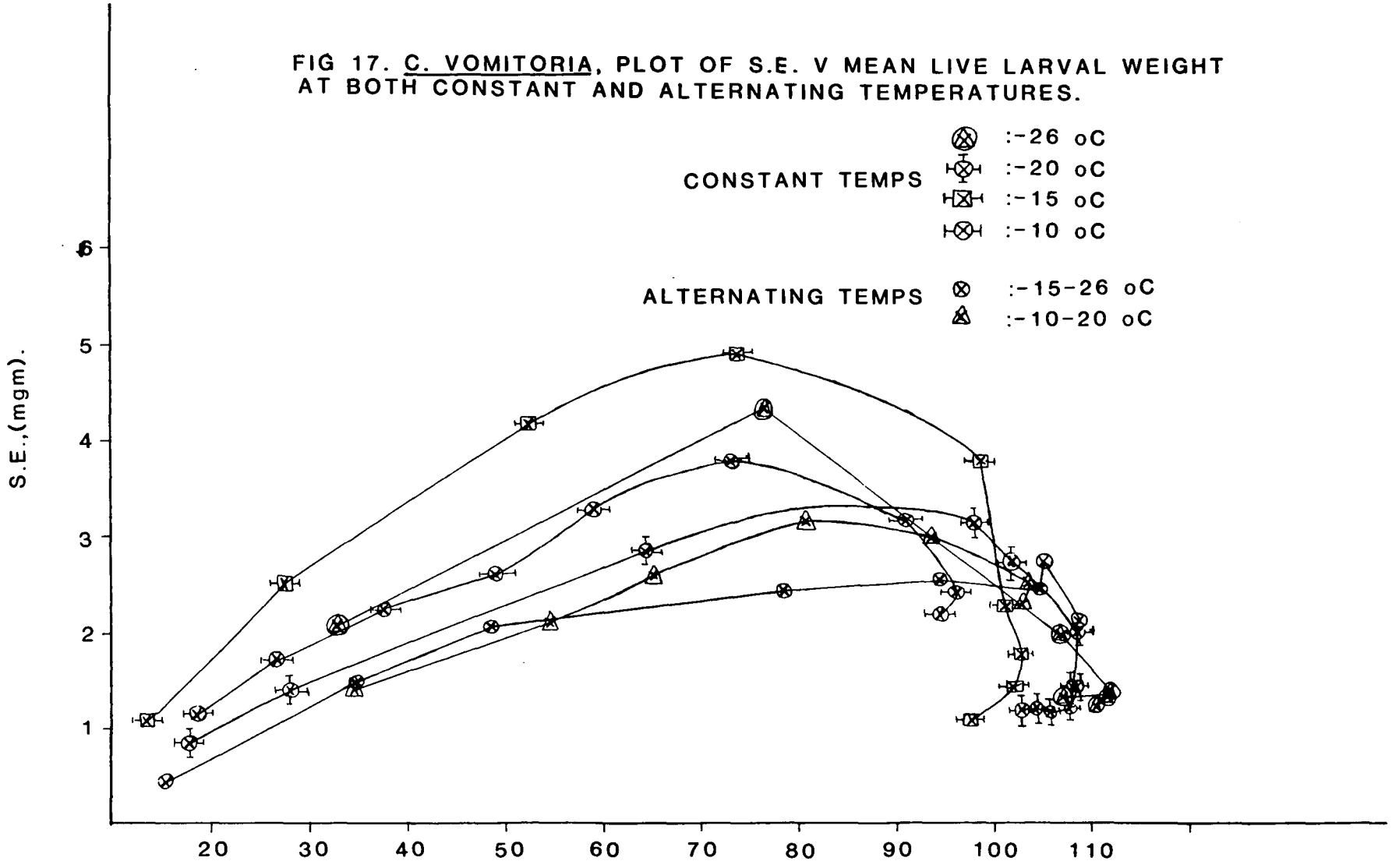
Not only do alternating temperatures affect the duration of the 3rd instar larvae, but also affect the individual weight heterogeneity within the 3rd instar (Fig. 17), which is shown by the large diferences in the S.E. between constant and alternating temperatures. The range of the maximum S.E. in the constant temperature series is 3.14 mg - 4.90 mg, whereas in the alternating temperature series is 2.74 mg - 3.16 mg (see Fig. 17).

The rate of development is faster at the alternation 10° - 20° compared to a constant 15°, as shown by the day-degree requirement on Table 33, therefore the alternation in temperature is synchronising the growth of the larvae, as shown by a large reduction in the S.E. and Coefficient of variation for the larval development from a constant 15° in Table 10, to the alternation 10° - 20° in Table 31.

The rate of development at the alternation 15° - 26° is very similar to that of a constant 20° as shown by the day-degree requirement in Table 33. So at the higher alternating temperatures it would appear that C. vomitoria has a more linear relationship with temperature.

The results for C. vomitoria under constant and alternating temperature conditions show how fluctuations in temperature can be

FIG 17. C. VOMITORIA, PLOT OF S.E. V MEAN LIVE LARVAL WEIGHT AT BOTH CONSTANT AND ALTERNATING TEMPERATURES.



Note: Successive points in time have been joined up.

as important as the average temperature used in the experiment. Comparing the day-degree requirement at a constant 20° to that at an alternation 10° - 20°, i.e. where the average temperature is much lower (15°), in (Table 33), one can see that infact C. vomitoria develops faster at the alternating temperatures which have a lower average temperature, showing that within this range, fluctuations in temperature rather than a higher average temperature increase developmental rate, especially in the 3rd instar larvae.

Watt (1968) cited by Hanski (1977) considers that we ought to be able to understand the effects of temperature fluctuations, "by summing the effects at each of the temperatures experienced, as each of the effects would be predicted from a curve for the effect of constant temperature." This statement may hold true with other species, but in the case of C. vomitoria, as can be seen from the comparison made above, one cannot predict the developmental rate in the alternating temperature series from the constant temperature series.

Considering Pradhan's theory, as explained previously (page 40), one can understand why an alternation between 10° - 20° with C. vomitoria develops faster than at a constant 15°, assuming that this range is in the lower foot of the curve. However, Pradhan's theory falls down when you compare an alternation between 10° - 20° with a constant 20°, in this case according to Pradhan's theory, development should be faster at the constant 20°, because although with alternating temperature you have accelerative and retardative effects, the overall effect would be retardative as compared to a constant 20°. Pradhan does not take into account that the fluctuation in temperature may by more important, within a fixed range, than a higher constant temperature, which is the case I found with C. vomitoria.

Lucilia sericata larvae reared under conditions of alternating temperatures.

The larvae of L. sericata were reared under conditions of alternating temperatures, (10° - 20° and 15° - 26°), as described on page 8. The results from these experiments are set out on Tables 34 and 35, and Fig. 18, (pages 46a-c, following this page).

The duration of egg incubation, 1st instar, 2nd instar and 3rd instar up to maximum mean weight were noted at each of the two temperatures used in each experiment, (Table 36, page 46d.), the method for determining egg incubation and the larval moults is the same as used for the constant temperature series as described on pages 5 and 7 respectively.

I then calculated the day-degree requirement for each of these stages under the different conditions of alternating temperatures, using the calculated zero of development of 10.1° from the constant temperature experiments, see page 27. These results were then compared to those from the constant temperature series on Table 37.

Table 37 - Lucilia sericata, a comparison of the day-degree requirement of eggs and larvae to maximum mean weight at constant and alternating temperatures.

	15°	10°-20°	20°	15°-26°
Egg incubation	9.2	12.0	9.9	10.4
1st instar	13.4	10.0	14.2	12.2
2nd instar	14.2	10.8	17.1	13.1
3rd instar	22.7	18.8	20.6	28.5
Total	59.5	51.6	61.8	64.2

FIG 18. L. SERICATA ,LARVAL DEVELOPMENT UNDER CONDITIONS OF ALTERNATING TEMPERATURES BETWEEN 10oC-20oC AND 15oC-26oC.

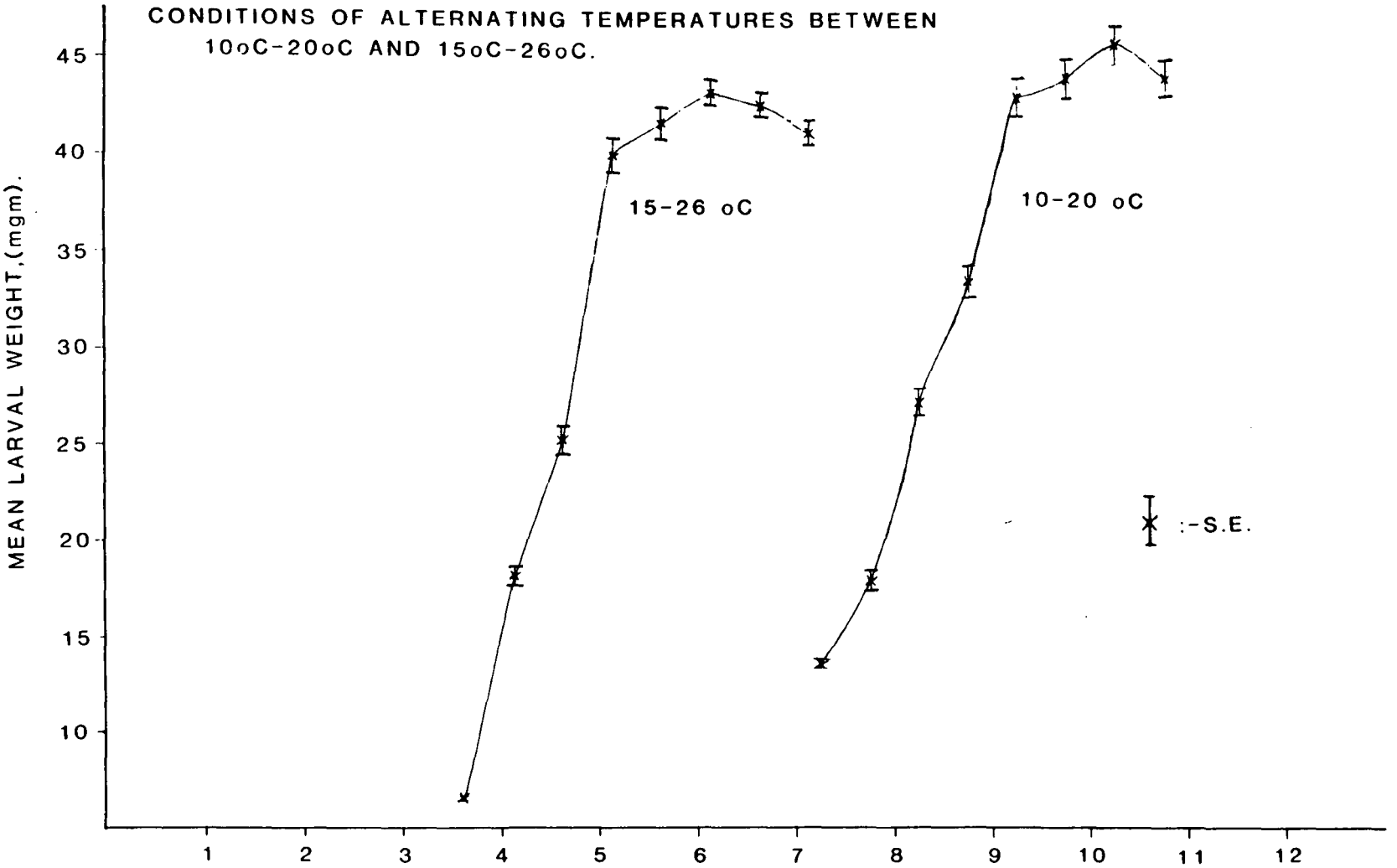


Table 34 *Lucilia sericata*, larval development as mean live weights (mgm) under conditions of alternating temperatures between 15°C - 26°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
						15°C	
3.62	6.56	1.78	1.33	0.14	20.4	26°C	95
4.12	18.16	25.47	5.05	0.52	27.8	15°C	93
4.62	25.24	53.54	7.32	0.76	29.0	26°C	93
5.12	39.91	72.70	8.53	0.89	21.4	15°C	92
5.62	41.60	74.96	8.66	0.90	20.8	26°C	92
6.12	43.12	43.66	6.61	0.69	15.3	15°C	91
6.62	42.45	38.72	6.22	0.65	14.7	26°C	91
7.12	41.12	36.44	6.04	0.64	14.7		90

Table 35 *Lucilia sericata*, larval development as mean live weights (mgm) under conditions of alternating temperatures between 10°C - 20°C.

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
						20°C	
7.23	13.69	13.37	3.66	0.38	26.7	10°C	92
7.73	17.98	28.76	5.36	0.55	29.8	20°C	95
8.23	27.18	44.90	6.70	0.71	24.6	10°C	90
8.73	33.45	62.48	7.90	0.84	23.6	20°C	89
9.23	42.93	76.53	8.75	0.94	20.4	10°C	87
9.73	43.90	87.64	9.36	1.00	21.3	20°C	88
10.23	45.76	79.85	8.94	0.96	19.5	10°C	87
10.73	44.01	69.27	8.32	0.89	18.9		87

Table 36 *L. sericata*, duration of egg and larval stages

under different conditions of alternating temperatures.

Alternating temperatures of experiment	Time of egg laying, (placed at higher of two temps.).	Egg Incubation, time at each temperature.	Ist Instar, time at each temperature.	2nd Instar, time at each temperature.	3rd Instar until maximum mean weight, time at each temperature.
15° - 26°	6.00 p.m.	12 hrs. at 26° plus 12 hrs. at 15°	14.75 hrs. at 26° plus 12 hrs. at 15°	12.5 hrs. at 26° plus 24 hrs. at 15°	35.75 hrs. at 26° plus 24 hrs. at 15°
10° - 20°	3.30 p.m.	29.25 hrs. at 20° plus 24 hrs. at 10°	24.25 hrs. at 20° plus 33 hrs. at 10°	26.25 hrs. at 20° plus 27 hrs. at 10°	45.75 hrs. at 20° plus 36 hrs. at 10°

It can be seen from Table 37, that when you compare the alternation of temperature 15° - 26° with a constant 20°, that egg incubation has a thermal requirement which remains about the same at both constant and alternating temperatures. However, the 1st and 2nd instars develop slightly faster at alternating temperatures and the 3rd instar slower. This appears to be a good example of how different stages react to temperature in different ways, but further investigation is required before a definite statement could be made. However these differences occur, the overall total thermal requirement remains about the same at the alternation 15° - 26° as at a constant 20°.

When comparing the alternation of temperature 10° - 20° with a constant 15°, it is found that an alternation of temperature decreases the thermal requirement and hence increases the rate of development in the 1st, 2nd and 3rd instars, but increases the thermal requirement of egg development, which is slower at alternating temperatures. So the overall total thermal requirement is lower at alternating temperatures than at a constant temperature.

This lowering of the thermal requirement in the 1st, 2nd and 3rd instars at the alternation 10° - 20°, indicates that there is some development taking place at 10°, although it is slightly below the threshold for development of 10.1° from the constant temperature series. Ludwig (1928) on his investigations on the pupae of Drosophila melanogaster found that as a result of alternating temperatures, one of which lay below the threshold, a degree of acceleration which he considered was due to a certain amount of development taking place even at the low temperature. He alternated temperatures of 7°, 8°, 9° and 10° with 20°, and found that although 8° was below the theoretical threshold of development of the insect, the pupae showed a 5% acceleration in development. But when the pupae were exposed to alternating temperatures of 7° and 20°, the rate of development was the same as

that at a constant temperature of 20°.

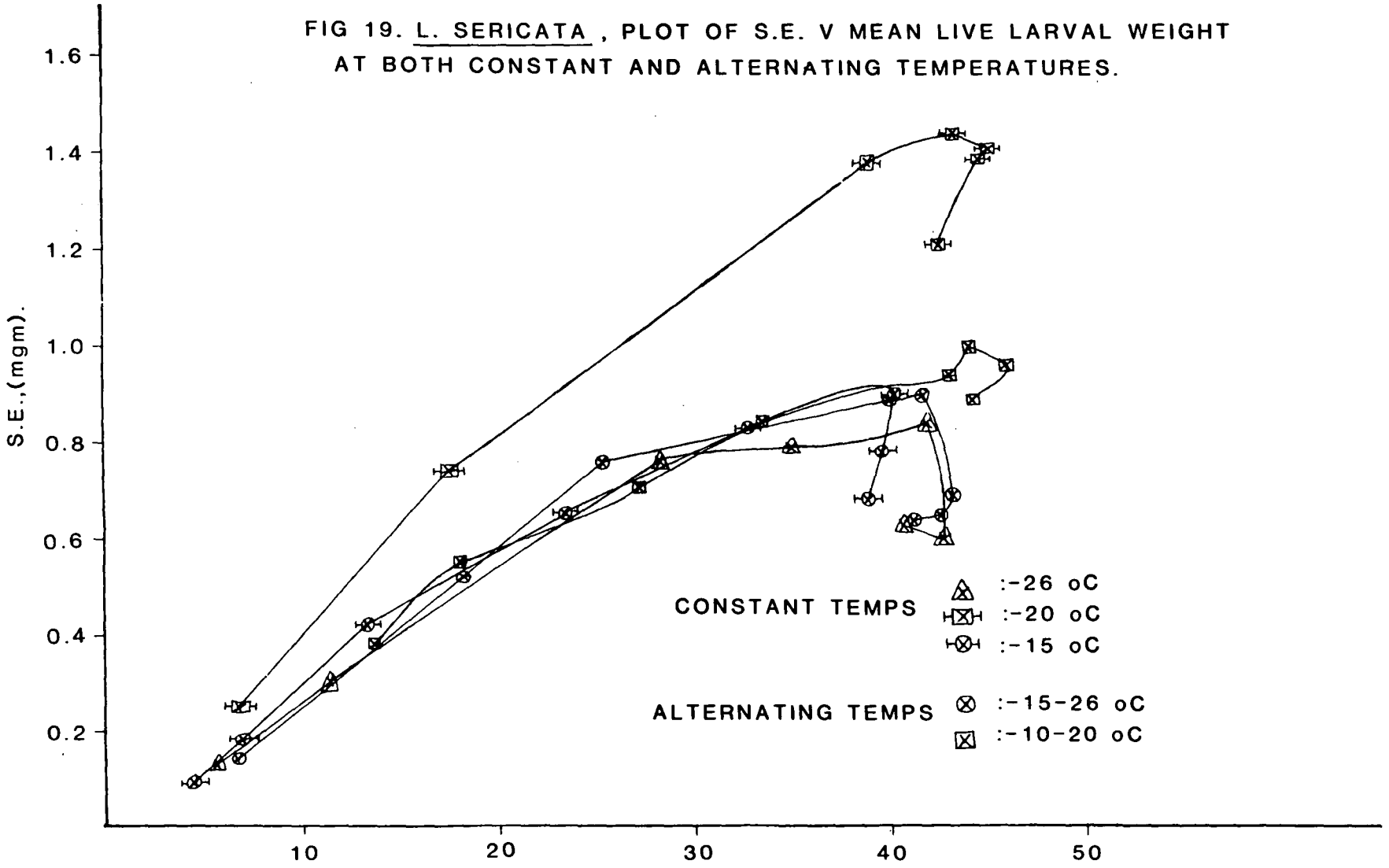
I found in the cases of both C. vicina and C. vomitoria that alternating temperatures affected the individual weight heterogenity, which was shown by the large differences in the S.E. between constant and alternating temperatures (Figs. 15 and 17). However, with L. sericata I found that the S.E. was very similar throughout larval development at both constant and alternating temperatures, except at a constant 20°, as shown on Fig. 19.

The fact that the S.E. remains comparable throughout larval development at both constant and alternating temperatures, indicates that it is independent, within fixed limits, of temperature changes, i.e. fluctuations in temperature, and more dependent on the day-degrees above the zero for development to which the larvae have been exposed. This might well be the key to explain why the developmental rate at alternating temperatures is more predictable from constant temperature results with L. sericata, than with C. vicina or C. vomitoria, assuming that the higher S.E. at a constant 20° is exceptional in this case.

The view of Watt (1968), cited before appears to hold true to a much larger degree with L. sericata than with C. vicina or C. vomitoria; whether it follows Watt's reasoning as a summation of the effects, or if it is chance that alternating temperatures have affected different stages to varying degrees, giving approximately the same total thermal requirement for development, especially at the higher alternation of 15° - 26°, requires further investigation.

Chapman (1931) cited by Ahmad (1936) emphasised that while it was not wise to make generalizations which would apply to all animals, and here I would add "stages and larval stages", it seemed very likely that temperature behaviour of an organism would correspond to the ecological conditions to which it was adapted in a state of nature.

FIG 19. L. SERICATA , PLOT OF S.E. V MEAN LIVE LARVAL WEIGHT AT BOTH CONSTANT AND ALTERNATING TEMPERATURES.



Note: Successive points in time have been joined up.

Considering Pradhan's theory, as explained previously on page 40, in the case of L. sericata, one can see that the alternation of temperature between 15° - 26° is marginally slower in development that at a constant 20° (Table 37). According to Pradhan's theory, this would suggest that the higher of the two alternating temperatures, i.e. 26°, is entering into the top of the sigmoid curve, and this is having a retardative affect. The reverse happened when I used 10° - 20°, where the alternation of temperature 10° - 20° develops faster than at a constant 15°. This would indicate that the temperature of 10° is in the foot of the curve, hence the alternation 10° - 20° is having an accelerative effect compared to a constant 15°.

Although a comparison of constant to alternating temperatures with L. sericata appears to fit more closely both the theories of Watt (1968) and Pradhan (1945), I would argue that the fact that alternating temperatures affected hatching and the different larval stages to differing degrees, indicates that one cannot look at larval development as a whole, but that we have to look upon each stage as a different organism.

Phormia terrae-novae larvae reared under conditions of alternating temperatures.

The larvae of P. terrae-novae were reared under conditions of alternating temperatures, (15° - 26° and 10° - 20°), as described on page 8. The results from these experiments are set out on Tables 38 and 39, and Fig. 20, (pages 50 a-c, following this page).

The duration of egg incubation, 1st instar, 2nd instar and the 3rd instar up to maximum mean weight were noted at each of the two temperatures used in each experiment, (Table 40, page 50d), the method for determining egg incubation and the larval moults is the same as used for the constant temperature series as described on pages 5 and 7 respectively.

I then calculated the day-degree requirement for each of these stages under the different conditions of alternating temperatures, using the calculated zero for development of 10.1° from the constant temperature experiments, (see page 32). These results were then compared to those from the constant temperature series on Table 41.

Table 41 - Phormia terrae-novae, a comparison of the day-degree requirement of eggs and larvae up to maximum mean weight at constant and alternating temperatures.

	15°	10°-20°	20°	15°-26°
Egg incubation	12.2	10.4	12.9	12.9
1st instar	26.2	21.5	26.5	18.8
2nd instar	30.0	27.8	32.9	21.9
3rd instar	41.3	43.4	49.1	38.8
Total	109.7	103.1	121.4	92.4

FIG 20. P. TERRAE-NOVAE LARVAL DEVELOPMENT UNDER CONDITIONS OF ALTERNATING TEMPERATURES BETWEEN 10oC-20oC AND 15oC-26oC.

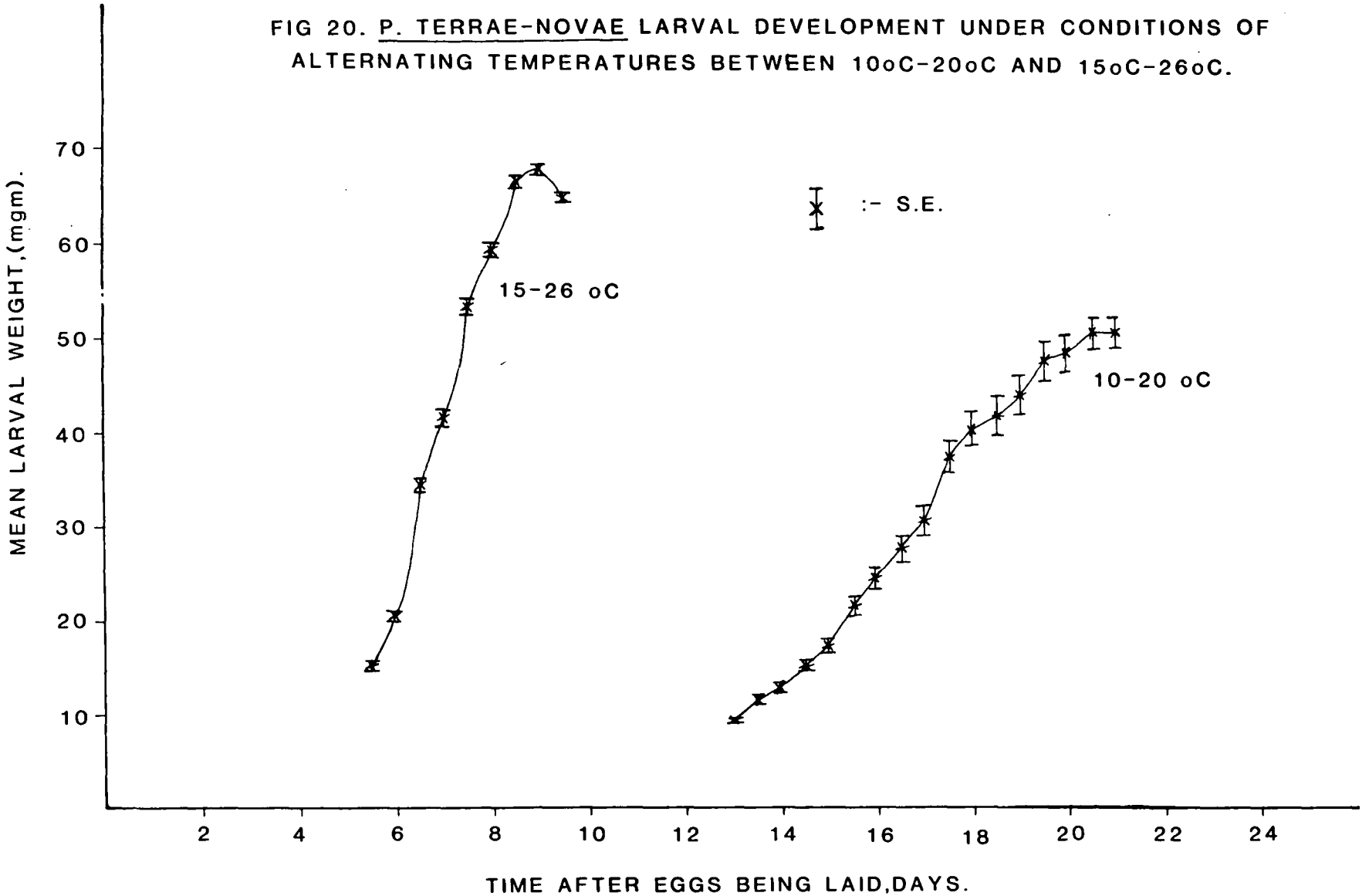


Table 38 Phormia terrae-novae, larval development as mean live weights (mgm) under conditions of alternating temperatures between 15°C - 26°C

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
						26°C	
5.44	15.28	15.38	3.92	0.42	25.7		86
						15°C	
5.94	20.66	27.98	5.29	0.57	25.6		86
						26°C	
6.44	34.42	48.70	6.98	0.75	20.3		86
						15°C	
6.94	41.63	61.51	7.84	0.85	18.8		86
						26°C	
7.44	53.24	54.33	7.37	0.79	13.8		86
						15°C	
7.94	59.21	49.36	7.03	0.76	11.9		86
						26°C	
8.44	66.62	38.94	6.24	0.67	9.4		86
						15°C	
8.94	67.73	32.49	5.70	0.61	8.4		86
						26°C	
9.44	64.83	32.64	5.71	0.62	8.8		84

Table 39 *Phormia terrae-novae*, larval development as mean live weights (mgm) under conditions of alternating temperatures between 10°C - 20°C

Time after hatching days	Mean weight	Variance	S.D.	S.E.	Coefficient of variation %	Temp. between weighings	No. larvae
						10°C	
12.94	9.38	10.04	3.17	0.34	33.8	20°C	89
13.44	11.55	25.55	5.05	0.55	43.8	10°C	85
13.94	12.81	29.97	5.47	0.62	42.7	20°C	79
14.44	15.17	45.84	6.77	0.77	44.6	10°C	77
14.94	17.16	62.03	7.88	0.92	45.9	20°C	74
15.44	21.79	91.62	9.57	1.13	43.9	10°C	72
15.94	24.63	106.44	10.32	1.25	41.9	20°C	68
16.44	27.91	141.19	11.88	1.44	42.6	10°C	68
16.94	30.65	175.37	13.24	1.62	43.2	20°C	67
17.44	37.47	226.46	15.05	1.88	40.2	10°C	64
17.94	40.29	220.24	14.84	1.88	36.8	20°C	62
18.44	41.89	236.12	15.37	1.95	36.7	10°C	62
18.94	44.01	238.03	15.43	1.98	35.1	20°C	61
19.44	47.84	225.63	15.02	1.96	31.4	10°C	59
19.94	48.47	214.03	14.63	1.92	30.2	20°C	58
20.44	50.91	198.35	14.08	1.88	27.7	10°C	56
20.94	50.98	179.91	13.41	1.79	26.3	20°C	56

Table 40 P. terrae-novae, duration of egg and larval stages under different conditions of alternating temperatures.

Alternating temperatures of experiment	Time of egg laying, (placed at higher two temps.).	Egg Incubation, time at each temperature.	Ist Instar, time at each temperature.	2nd Instar, time at each temperature.	3rd Instar until maximum mean weight, time at each temperature.
15° - 26°	10.30 a.m.	15.75 hrs. at 26° plus 12 hrs. at 15°	21 hrs. at 26° plus 24 hrs. at 15°	25.75 hrs. at 26° plus 24 hrs. at 15°	44 hrs. at 26° plus 48 hrs. at 15°
10° - 20°	10.30 a.m.	25.25 hrs. at 20° plus 24 hrs. at 10°	52.25 hrs. at 20° plus 48 hrs. at 10°	67.5 hrs. at 20° plus 72 hrs. at 10°	105.5 hrs. at 20° plus 96 hrs. at 10°

It can be seen from Table 41, that when you compare the alternation of temperature 15° - 26° with a constant 20°, that egg incubation has a thermal requirement which remains constant. However, the 1st, 2nd and 3rd instars develop much faster at alternating temperatures than at a constant 20°, hence the total development is much faster at the alternating temperature 15° - 26° than at a constant 20°.

Out of all four of the species used in these experiments, P. terrae-novae is the first to show a marked increase in the rate of development at the higher alternating temperature of 15° - 26° as compared to a constant 20°. C. vomitoria and L. sericata both showed approximately the same total thermal requirement for the alternation 15°-26° as at a constant 20°, although various stages showed an increase or decrease of developmental rate, at either constant or alternating temperatures. C. vicina developed faster at a constant 20° than at the alternation 15° - 26°, especially in the 3rd instar.

This shows that the development of P. terrae-novae is stimulated by fluctuations of higher temperatures, which is not found in the other 3 species used in the experiments. The finding that the development of P. terrae-novae is stimulated by the fluctuations at higher temperatures, is opposite to the theory put forward by Pradhan (1945), (see page 40), where one would expect a retardation at the alternation of higher temperatures, or at least no stimulation. The most one would expect, is that the thermal requirement would remain about the same as at a constant 20°. The finding is also contrary to the view of Watt (1968).

It would appear from Table 41, that it is not the constant temperatures experienced during the alternating temperatures 15° - 26° that is stimulating development, but infact is the amplitude and range within which the temperatures fluctuate, which is giving rise to the stimulation.

This view is put forward because of the following consideration:-

When comparing the alternation of temperature 10° - 20° with a constant 15°, it is found that this temperature alternation decreases the thermal requirement and hence increases the rate of development of egg incubation, 1st and 2nd instars, but increases the thermal requirement of the 3rd instar, which is slower at alternating temperatures (43.4 day-degrees versus 41.3). All of the above changes in thermal requirement are small, and the total thermal requirement is only slightly less at alternating temperatures 10° - 20° than at a constant 15°.

This lowering of the thermal requirement in egg incubation, 1st and 2nd instars, indicates that there is some development taking place at 10°, although it is slightly below the threshold for development of 10.1° from the constant temperature series, as found by Ludwig (1928) on his investigations on the pupae of Drosophila melanogaster (see page 47).

Considering Pradhan's theory, as explained previously, in the case of P. terrae-novae, an alternation of temperature 10° - 20° causes development to occur slightly faster than at a constant 15°. This would indicate that the temperature of 10° is in the foot of the sigmoid curve, hence the alternation 10° - 20° is having an accelerative effect compared to a constant 15°.

Watt's theory of summation of effects appears to hold true when comparing a alternation of 10° - 20° with a constant 15° with P. terrae-novae, as found with L. sericata. Again, whether it follows Watt's reasoning as a summation of the effects, or if it is chance that alternating temperatures have affected different stages to varying degrees, giving approximately the same total thermal requirement for development, requires further investigation.

Watt's theory of summation may hold true for some species, but is

unlikely to hold true for C. vomitoria, L. sericata and P. terrae-novae, because the results obtained from these species under conditions of constant and alternating temperature, show how fluctuations in temperature can be as important as the average temperature used in the experiment. Comparing the day-degree requirement at a constant 20° to that at an alternation between 10° - 20°, i.e. where the average temperature is much lower (15°), in Tables 33, 37 and 41, one can see that infact C. vomitoria, L. sericata and P. terrae-novae develop relatively faster at the alternating temperatures which have a lower average temperature. Showing that within this range, fluctuations in temperature rather than a higher average temperature increase developmental rate.

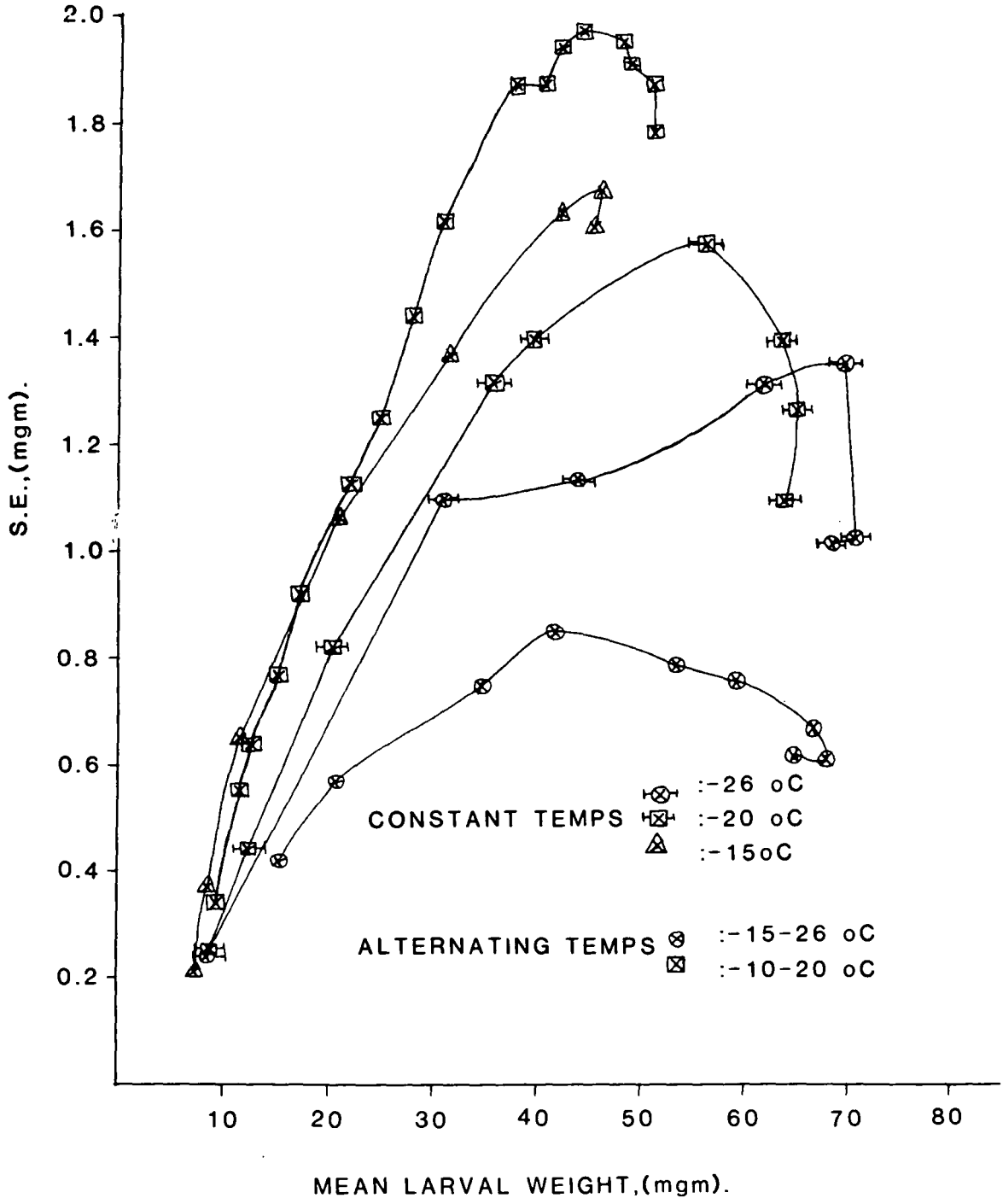
When one looks at the effect of alternating temperatures compared to constant temperature on the S.E. with P. terrae-novae, the picture is not as clear as with C. vicina, C. vomitoria or L. sericata. The following pattern was found in Fig. 21, where the S.E. of 10° - 20° > (15°) > (20°) > (26°) > (15° - 26°), which holds true throughout the weight range, except up to 20 mg mean larval weight, where at 15° the S.E. is slightly above that of 10° - 20°.

The above indicates that an alternation of temperature at lower temperatures gives a higher S.E., and at higher temperatures gives a lower S.E. with constant temperatures, the higher the constant temperature, the lower the S.E.

This indicates that high constant or alternating temperatures promote greater synchronization within a batch of larvae hatching at about the same time, than would a lower constant or alternating temperature.

The above results show how P. terrae-novae is adapted to higher temperatures, this adaptation and those of the other 3 species are looked into, in the following di scussion.

FIG 21. P. TERRAE-NOVAE PLOT OF S.E. V MEAN LIVE LARVAL WEIGHT AT BOTH CONSTANT AND ALTERNATING TEMPERATURES.



Note: Successive points in time have been joined up.

Discussion

The day-degrees required for development from the eggs being laid to maximum mean larval weight, under different conditions of both constant and alternating temperatures, for all four of the species used in these experiments are set out on Table 42.

Because I used the day-degree requirement above the zero for development for each of the four species, this does not mean that the smaller the thermal requirement the quicker to develop in time, because in using day-degrees the time factor has been removed; i.e. C. vicina develops faster at 26° than at 10°, but it requires more day-degrees to develop at 26° than at 10°.

It is reasonable to conclude that the temperature(s) at which a species has its lowest thermal requirement, is the temperature range to which the species is best adapted.

Most previous authors have sought to find the optimum temperature for development, meaning, that temperature which gives the shortest developmental time, which is not neccessarily the temperature to which the species is best adapted; with exceptions of authors like Peairs (1927) who realised the significance of the zero temperature for development and calculated the day-degrees above the zero for development at various temperatures.

Looking at the results obtained with L. sericata, Table 42, one can see that there appears to be a stimulation at the alternation 10° - 20°, in the way that this has the lowest thermal requirement for L. sericata, as compared to the other temperatures. This may well not be the case, because as discussed previously on page 47 there might well be some development taking place at 10°, which is below the zero for development, and so would not be accounted for in the day-degrees above the zero for development. So for L. sericata it

Table 42 - Day-degrees required for development from the eggs being laid to maximum mean larval weight at both constant and alternating temperatures, for all four species used in these experiments.

	10°	15°	20°	26°	5°-15°	10°-20°	15°-26°
Lucilia sericata	Did not complete development	59.5	61.8	59.6	-	51.6	64.2
Phormia terrae-novae	Did not complete development	109.7	121.4	86.0	-	103.1	92.4
Calliphora vicina	72.4	73.0	93.9	97.2	96.7	106.7	105.9
Calliphora vomitoria	111.2	117.7	113.8	113.8	-	88.2	110.1

appears as though the day-degree requirement remains fairly constant throughout the range of temperatures used in these experiments, except for a constant 10°, where L. sericata did not complete development. L. sericata larvae seem to be adapted to temperatures between 19° and around 27°, (Ash and Greenberg 1975), because below 19° or much above 27°, L. sericata tends to go into larval diapause.

Hepburn (1943) found that Lucilia species, including L. sericata, bred in carcasses during the winter and cooler months, but not in the summer in South Africa, and Denno and Cothran (1975) found that Phaenicia sericata (L. sericata) utilized carrion during the warm season in California. These findings agree with those of Ash and Greenberg (1975) that L. sericata larvae have a range of about 19° - 27°, above and below which they go into larval diapause. So my results indicate that L. sericata is adapted equally well to temperatures within this range.

The results obtained with P. terrae-novae, Table 42, show a stimulation at the alternation 15° - 26° and at a constant 26°, because at these temperatures P. terrae-novae has its lowest thermal requirement for development. This indicates that P. terrae-novae is adapted to high temperatures, i.e. above 20°, and the stimulation is greatest at a constant 26°, and I would suggest that the stimulation found at the alternation 15° - 26° is due to the time the larvae are developing at 26°, rather than the amplitude of the alternation.

The results obtained with C. vicina show a stimulation at the lower constant temperatures 10° and 15°, Table 42, because at these temperatures C. vicina has its lowest thermal requirement for development and is adapted to the lower temperature range. It is also interesting to note that, C. vicina from Table 42, at the alternation 5° - 15° has a lower thermal requirement than at the alternations 10° - 20° and 15° - 26°, and although the thermal requirement is still

considerably higher than at a constant 10° or 15°, this is also an indication of the adaptation of C. vicina to lower temperatures.

C. vomitoria showed a stimulation at the alternation 10° - 20°, Table 42, because at this alternation C. vomitoria had its lowest thermal requirement for development, and is adapted to temperatures alternating around this range of 10° - 20°.

Denno and Cothran (1975) state that many species such as C. vicina and C. vomitoria are strictly carrion breeders, whereas some species such as L. sericata and P. terrae-novae cross the boundaries and exploit carrion as well as causing myasis. This makes L. sericata and P. terrae-novae interesting species to study, to see what affect a change in the constant or alternating temperature does to the speed of larval development, compared to the effect on the Calliphora species. Deonier (1940) recorded that the Calliphora adults become active at around 1.7° whereas L. sericata became active at around 10°, which demonstrates Calliphora's ability to withstand lower temperatures.

The above results for the four species used in these experiments show how larval development is adapted in the different species to different temperature ranges. P. terrae-novae is adapted to temperatures above 20°, L. sericata to temperatures from around 15° to 26°, C. vicina to the temperature range 10° to 15° and C. vomitoria to temperatures alternating around the range 10° to 20°.

All four species will develop within the range of temperatures used in these experiments, with the exceptions of L. sericata and P. terrae-novae not completing development at 10°, but the larvae of each species has a specific temperature range to which it is best adapted.

An interesting fact to investigate is whether the temperature to which the species is best adapted to, affects all the larval instars equally, or whether it affects certain larval instars more than the

others.

Considering the stimulation in development in day-degrees at the lower constant temperatures of 10° and 15° with C. vicina, one can see from Table 7 that the 3rd instar has a lower thermal requirement at both 15°C and 10°C than at the other temperatures used in these experiments, so the adaptation occurs in the 3rd instar larvae of C. vicina.

In the case of C. vomitoria with the stimulation at the alternation 10° - 20° the thermal requirement is lower in the 3rd instar, Table 33, which gives rise to the quicker development than one would expect at this temperature range.

With L. sericata one finds a slight stimulation at the alternation 10° - 20°, and from Table 37 one can see that this lowers the thermal requirement of all three instars, which supports the argument that some development may be taking place at 10°.

In the case of P. terrae-novae one finds a stimulation at the alternation 15° - 26° and at a constant 26°; at the alternation 15° - 26°, Table 41, the thermal requirement of all three instars is lower, but this mainly occurs in the 2nd instar, and at a constant 26°, Table 24, the thermal requirement of the 2nd and 3rd instars are lower, but again mainly in the 2nd instar larvae.

The above findings agree with the statement made by Ash and Greenberg (1975), see page 37, and these are good examples of how adaptations in one part of the life cycle have a large affect on the life cycle as a whole.

Although one has to take great care when interpreting constant temperature results, and experiments carried out under unnatural conditions, to conditions the various species normally encounter, one can from these results make tentative suggestions.

One would expect an adaptation to show some reproductive advantage. I would suggest that the fact that each of the four

species used in these experiments appears to have a temperature range to which each is best adapted, separates the four species thermally, as it is not uncommon to find all four of these species inhabiting the same geographical area. This 'thermal separation' reduces competition between these species and so will increase survival, as they will each have their own niche. Because as we can see from the results C. vicina and C. vomitoria will not be able to compete with L. sericata and P. terrae-novae at the higher temperatures, and so must occupy cooler parts of the habitats, i.e. higher in the mountains and moors, and cooler parts of the seasons so maybe giving rise to seasonal succession. L. sericata and P. terrae-novae will not develop below 10°, but at these temperatures both C. vicina and C. vomitoria will develop quite successfully.

The fact that C. vicina and C. vomitoria can stand and develop at much lower temperatures than L. sericata or P. terrae-novae is already a well known fact, as shown by Cragg (1956), when he studied the action of climate on the larvae, prepupae and pupae of certain blowflies, which included the four species used in my experiments.

When one considers that the food source for the development of the larvae of these species are mainly carcasses, which are limited and very temporary, the importance of the separation of these species thermally into different niches is very obvious, and hence a degree of co-existence between these necrophagous fly species is achieved. The importance of niches for various species was shown well by Denno and Cothran (1975), where several species exploited the same areas at different times of the year, hence reducing competitive interactions.

Although more factors are involved in competition between species than just developmental rate, it is never-the-less a very important factor, and it is very important to determine the temperature range to to which each species is best adapted, before one can realistically compare one species to another.

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Appendix 1

Analysis of the dispersion of larval development rates and amounts, in terms of the quartiles of the frequency distributions of larval weights.

As noted in the previous chapters (pages 12, 37, 44, 48 and 53) there was considerable variation in larval development rates and final weights achieved within each batch. This was true at various temperatures and all 4 blowfly species, and attention has been drawn to the actual size of this variation in terms of the S.E. and the Coefficient of variation in the tables and graphs already presented, and in samples of the frequency distribution of larval weights at constant 15° (pages 18, 24, 30, 34 and figs. 4, 7, 10 and 13).

In this Appendix the extent and nature of this variation in growth rates and amounts within sets of larvae that hatched within 30 minutes of each other, is further documented by examining separately the 4 quartiles of the frequency distributions of *C. vicina* larval weights at constant 20° and alternating 15° - 26° as examples.

It should be noted that in compiling the quartiles for calculating their means it was noticed that, from examination of the full frequency distributions, there was no evidence of any appreciable "leap-frogging" in larval weight changes. That is to say a group of say 8 larvae appreciably behind the rest within a quartile at one weighing, could usually be distinguished as laggards at the next weighing and so on.

The mean weight for each separate quartile, (1 the lowest or smallest in size, and 4 the highest or largest in size) are given in Tables 43 and 44. Also tabulated are these means in terms of the percentages of the maximum mean weight achieved by the highest (No. 4) quartile. These percentages thus give a measure of the extent to which the quartiles lag in terms of their weights, with of course the

highest quartile actually eventually achieving the highest mean, namely 100 per cent. These percentages are graphed in Figs. 22 and 23.

As noted in the Methods (page 5) in all larval rearing an excess of liver was provided so that when larval growth was completed and crops were emptied, there was always apparently an appreciable amount of liver that remained unused. Figs. 22 and 23 illustrate the fact that despite an excess of liver, many larvae, namely those of the lower 3 quartiles, do not achieve anything like the maximum mean weight of the upper quartile. The lower 2 quartiles particularly show little or no sign of catching up with the larger larvae during the later period, and indeed the two lower quartiles in general slowed and stopped their weight gain at much the same time as the upper quartiles. (There is some sign of continued growth for a time in quartiles 1 and 2 in Fig. 22 after the upper 2 quartiles completed weight gain, but this phenomenon was rather limited).

Although some of the slower developing larvae may have been infected with some micro-organism (? virus) that caused their slow development, this does not seem to be the whole explanation of this phenomenon of big scatter in growth rate and amount. Although some larvae died and disappeared from the sequence of weighings throughout the batch's growth, the numbers used at the different weighings that produced Tables 43, 44 and Figs. 22 and 23 show that very few were so lost. In Table 43 it is seen that after 3.81 days only 4 out of 52 larvae died, so that most slow developing larvae survived and eventually pupated, at a low final weight. It has also been noticed in routine blowfly culture for laboratory maintenance that it is normal, under laboratory conditions at any rate, for some larvae to lag behind others and to leave the carcass or equivalent larval feeding medium after the others and for these laggards to be noticeably

FIG 22. PERCENTAGE OF MAXIMUM MEAN WEIGHT OF HIGHEST QUARTILE (No.4,96.33mgm) V TIME AFTER HATCHING IN DAYS,FOR C.VICINA AT A CONSTANT 20oC

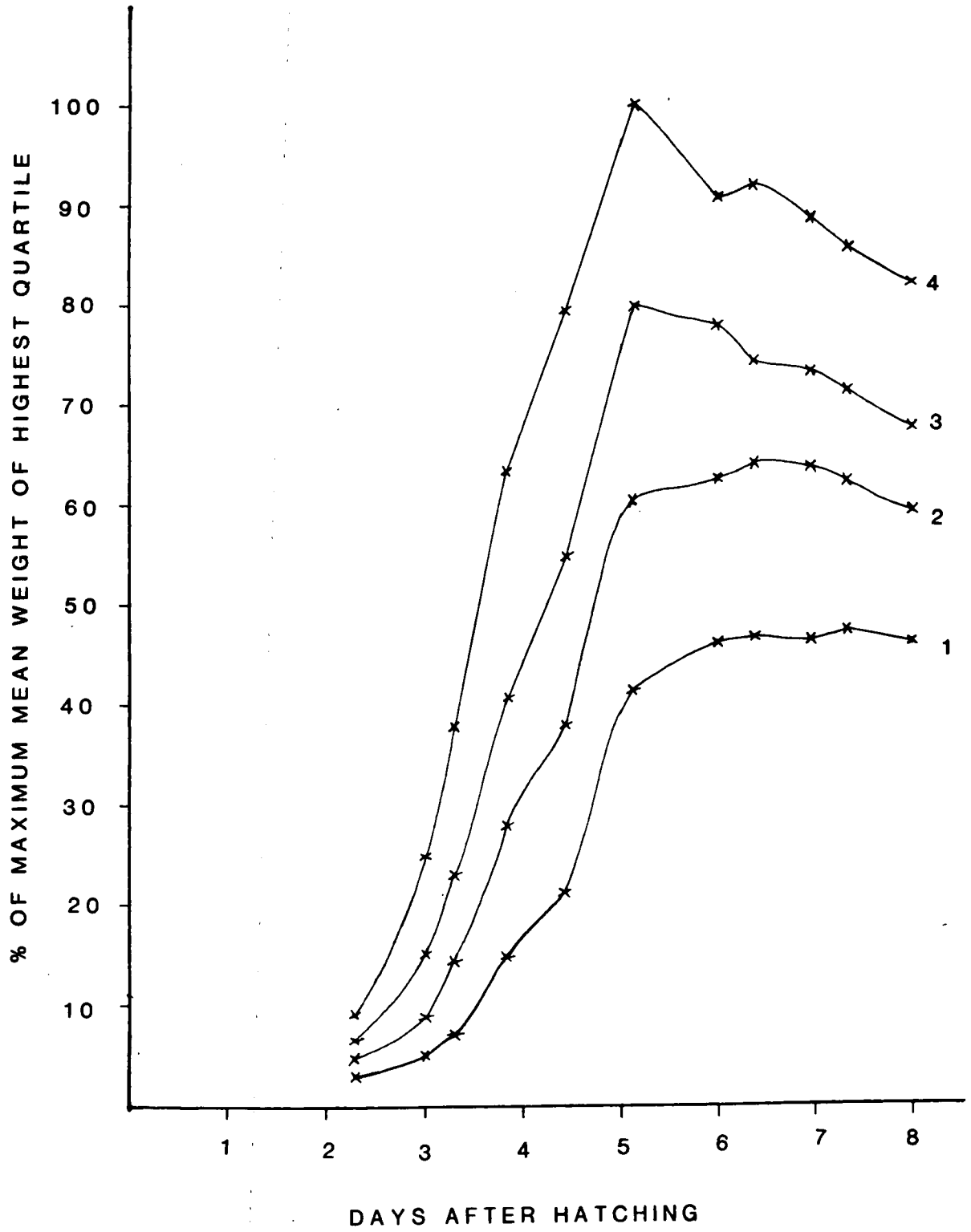

FIG 23. PERCENTAGE OF MAXIMUM MEAN WEIGHT OF HIGHEST QUARTILE (No.4,80.08mgm) V TIME AFTER HATCHING IN DAYS, FOR C.VICINA AT THE ALTERNATION 15o-26oC.

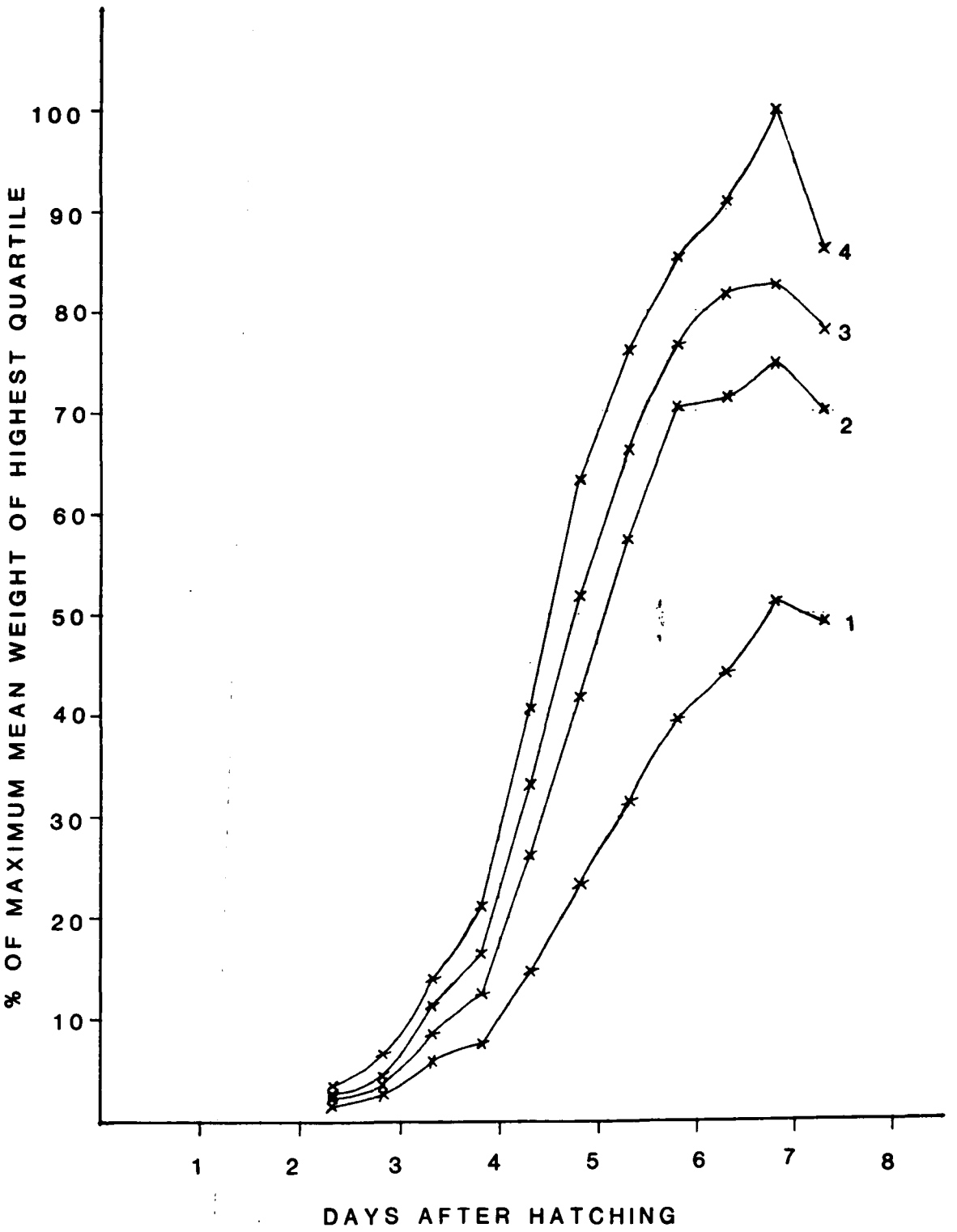

Table 43 - C. vicina constant 20°C. Larval frequency distributions divided into quartiles, giving the mean weight of each quartile, and the percentages of the maximum mean weight of the highest quartile at successive weighings.

Time after hatching, days	n	Means of quartiles					% of max. mean wt. of upper quartile				
		$\bar{x}$	1	2	3	4	$\bar{x}$	1	2	3	4
2.27	35	5.52	2.84	4.50	6.34	8.74	5.7	2.9	4.7	6.6	9.1
3.00	29	14.13	4.85	8.57	14.57	24.00	14.7	5.0	8.9	15.1	24.9
3.29	29	20.91	6.86	14.00	22.28	36.50	21.7	7.1	14.5	23.1	37.9
3.82	28	35.88	14.28	27.00	39.43	61.00	37.2	14.8	28.0	40.9	63.3
4.43	28	47.05	20.43	36.57	52.86	76.43	48.8	21.2	38.0	54.9	79.3
5.12	27	67.11	40.00	58.14	76.86	96.33	69.7	41.5	60.3	79.8	100
6.00	27	67.73	44.42	60.28	75.14	87.50	70.3	46.1	62.6	78.0	90.8
6.37	27	66.34	45.00	61.71	71.57	88.67	68.9	46.7	64.1	74.3	92.0
6.96	27	65.27	44.85	61.43	70.71	85.50	67.7	46.5	63.8	73.4	88.7
7.32	27	63.95	45.71	60.00	68.86	82.67	66.4	47.4	62.3	71.5	85.8
8.09	27	61.45	44.57	57.28	65.28	79.33	63.8	46.2	59.5	67.8	82.3

Table 44 - C. vicina alternating temperature 15° - 26°C. Larval frequency distributions divided into quartiles, giving the mean weight of each quartile, and the percentages of the maximum mean weight of the highest quartile at successive weighings.

Time after hatching, days	n	Means of quartiles $\bar{x}$	1	2	3	4	% of max. mean wt. of upper quartile $\bar{x}$	1	2	3	4	Temp. between weighings
2.31	74	2.08	1.31	1.84	2.23	2.92	2.(	1.6	2.3	2.8	3.6	
2.81	70	3.30	2.22	2.78	3.63	5.39	4.1	2.8	3.5	4.5	6.7	15°
3.31	51	8.03	4.78	6.92	9.07	11.28	10.0	6.0	8.6	11.3	14.1	26°
3.81	52	11.61	6.07	10.11	13.25	16.99	14.5	7.6	12.6	16.5	21.2	15°
4.31	52	23.39	11.77	21.00	26.61	32.54	29.2	14.7	26.2	33.2	40.6	26°
4.81	51	36.03	17.92	33.46	41.46	50.67	45.0	23.4	41.8	51.8	63.3	15°
5.31	50	46.61	25.31	45.92	53.00	60.92	58.2	31.6	57.3	66.2	76.1	26°
5.81	50	54.70	31.61	56.42	61.25	68.23	68.3	39.5	70.4	76.5	85.2	15°
.31	50	57.93	35.38	57.08	65.33	72.69	72.3	44.2	71.3	81.6	90.8	26°
.81	48	60.78	41.00	59.91	66.08	80.08	75.9	51.2	74.8	82.5	100	15°
7.31	48	57.30	39.42	56.17	62.58	69.00	71.(	49.2	70.1	78.1	86.2	26°

smaller in size.

This phenomenon of large scatter in development rates and amounts within blowfly larval batches is clearly worthy of further investigation, with a view of explaining the nature and causation of it. Since blowfly larvae produce a liquid medium containing digestive enzymes from their own mid-guts, the question arises as to whether the faster developing larvae might produce some substance(s) that retard the growth of their fellows? The same possibility might account for the fact that these retarded larvae cease growth before exhaustion of the food source, as noted above. The size and changes in the S.E. in the different species under various temperature regimes may reflect the operation of such intra-group effects produced by what would be essentially pheromones.

Another factor contributing to the scatter of development could of course be genetical variation between individuals. This would appear to me to be unlikely to be a major contribution to the phenomenon because in the routine procedure of blowfly culturing in the laboratory, and in the method of obtaining the 40 - 90 eggs or so in each batch used in these growth measurements, are all likely to produce rather a high degree of genetic uniformity in the blowfly cultures. For example it is quite likely from the routine methods used that many or all of the eggs used in a particular growth batch were laid by one female. So the fast and slow growing larvae are likely to include actual siblings from one pair of parents, which in turn had been subject to the same inbreeding regime. In order to investigate this genetical explanation, experiments involving segregation and breeding from the slower and faster developing larvae are clearly indicated and would be eminently practicable.

The analysis by quartiles at constant 20° and alternating 15° - 25° (Table 43, 44 and Figs. 22 and 23) illustrate again another

phenomenon discussed earlier (Table 29 and page 36). This is the way in which C. vicina larvae reached maximum mean weight much quicker at a constant 20° (5.12 days) than at the alternating temperature of 15° - 26° (6.81 days) despite the roughly equal amount of heat in day-degrees per day under both regimes. It is interesting to note that this was the case for all 4 quartiles. As shown previously and discussed on page 36, the slower development at the alternating temperatures was due to retardation in the third instar larva, while egg incubation and growth of the first two instars had the same thermal requirement under both regimes.

What ever the physiological explanation for the scatter in blowfly larval development documented here, as discussed earlier (pages 37 - 38) the scatter would have various effects in nature, including possibly reducing the amount of intra-specific larval competition, and reducing risks of disaster in the highly ephemeral carcass environment, by atleast ensuring that the fast developing minority achieve pupation in the race against time. The scatter in development may also of course be adaptive in the sense that blowfly females cannot apparently gauge their oviposition activity to the size of carcass available.