THE BIOLOGY AND TEMPERATURE-DEVELOPMENTAL TIME RELATIONSHIPS OF SEVERAL SPECIES OF MUSCOID FLIES

by

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INTRODUCTION

Field background

Different species of muscoid flies attain peak prevalence at different seasons of the year. Some species may be characteristically "warm weather" flies; certain others may be typically "cool weather" flies. Some species may be prevalent over a wide temperature range. Such observations, although highly important, yield no clue as to the adaptations which effect species perpetuation and seasonal recurrence, nor do they account for predominance of certain species over others. A great deal of biological information is prerequisite to a better understanding of these phenomena. Much of the biological data for this particular study was obtained while the writer was employed with the U. S. Public Health Service. A brief review of that background is included as a preface to the statement of the problem and the objectives of this study.

In 1948, the U. S. Public Health Service, through its Communicable Disease Center in Atlanta, Georgia, established Fly Control Projects in five metropolitan areas in the United States. These projects were established in order to determine the possible relationships of domestic flies in the transmission of poliomyelitis. The cities selected were Phoenix, Arizona; Topeka,

Kansas; Charleston, West Virginia; Troy, New York; and Muskegon, Michigan.

The Phoenix project was the only one that remained active through the expectancy period of five years. The writer was assigned to this project at its beginning in 1948, and his duties as Area Entomologist included the entomological evaluation of the control program through organization and supervision of surveys designed to guide, as well as to evaluate the control effort.

At the outset, it was evident that the Phoenix area presented a difficult problem in municipal fly control. Its fly season extended through 10-12 months, and its fly potential one of enormous magnitude. Entomologists connected with the project realized, early in the program, the need for more extensive data on the life histories and habits of flies indigenous to the area. However, it was not until after the failure of insecticidal measures in 1949 (48, p.807) that the entomological research program was instituted. The position of Research Entomologist was set up on July 24, 1950, and the writer occupied that position from the time it was set up until June 1, 1953, at which time he resigned his position to complete work toward an advanced degree at Oregon State College.

By June, 1953, a report had been prepared on the "Biology of Ten Species of Flies Common to Phoenix, Arizona". At the time of submission of the report it was evident that certain facets of the study could merit further investigation under controlled conditions. By clearance through the Director, Communicable Disease Center,

and permission of Dr. P. O. Ritcher, Head of the Department of Entomology at Oregon State College, authority was granted so that these investigations could be extended while the writer was in residence at Oregon State College, and the combined investigations used as thesis material.

Immediate background

Since coming to Oregon State College, the writer has been responsible for the rearing of test insects used in biochemical and toxicological studies on the campus. Colonies of Phormia regina are being reared on synthetic media, and both susceptible and resistant strains of houseflies are maintained. These, in addition to the laboratory rearings under constant temperature conditions, constitute a valuable source of data which augment the field studies conducted before coming to Oregon State College.

STATEMENT OF THE PROBLEM

Bimodal curve descriptive of total fly populations

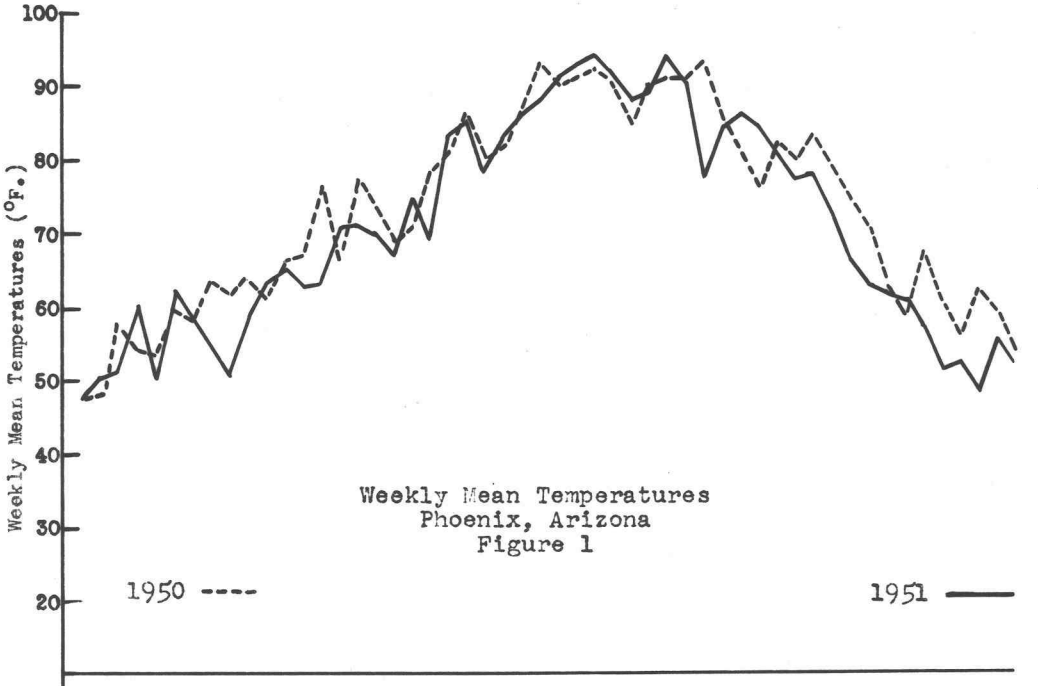
Total fly population curves, based upon data obtained by use of the Scudder grill (50, p.686) were typically bimodal in effect. Variations from this typical pattern were known to occur, as in 1950. In that year, peaks occurred in spring and fall, but the highest adult fly densities occurred in July. In 1952 the fall peak was almost entirely eliminated by control efforts. However,

judging from data obtained in 1951, 1953, the situation which prevailed in the fall of 1948, together with observations of local health officials in previous years, the overall typical pattern consisted of an initial peak in May followed by a summer slump which extended into October, and then a secondary peak which was abruptly cut off at the onset of cool weather on or about December 1. The fly population curves for 1950 and 1951, each based upon approximately 9,500 grill surveys, are shown in Figure 2.

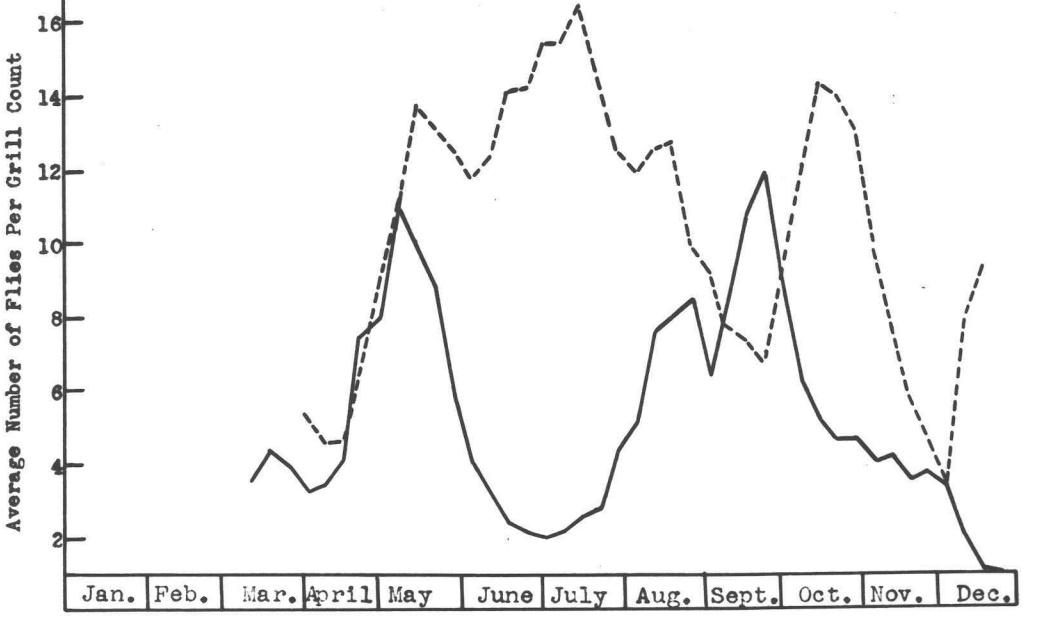
By comparing Figures 1 and 2, it may be noted that variations in summer trends of adult fly densities are not associated with differences in temperature. The reasons for this bimodal curve effect and its attendant variations were not clearly established. An analysis of the biological and ecological factors responsible for these effects is therefore considered as the first objective of this study.

Three types of seasonal prevalence

Twenty-eight species of flies were recovered from trap samples. Of these, less than ten species were considered as common. They included the following: Musca domestica Linnaeus (the common housefly); Phaenicia sericata (Meigen) (the green-bottle fly); Phaenicia pallescens (Shannon); Callitroga macellaria (Fabricius) (the secondary screwworm fly); Phormia regina (Meigen) (the black blowfly); Muscina stabulans (Fallen) (the false stablefly); Sarcophaga spp. (fleshflies); and Eucalliphora lilaea (Walker). With regard to seasonal prevalence, there were three types of flies



Weekly Mean Temperatures
Phoenix, Arizona
Figure 1



Adult Fly Densities
Phoenix, Arizona
Figure 2

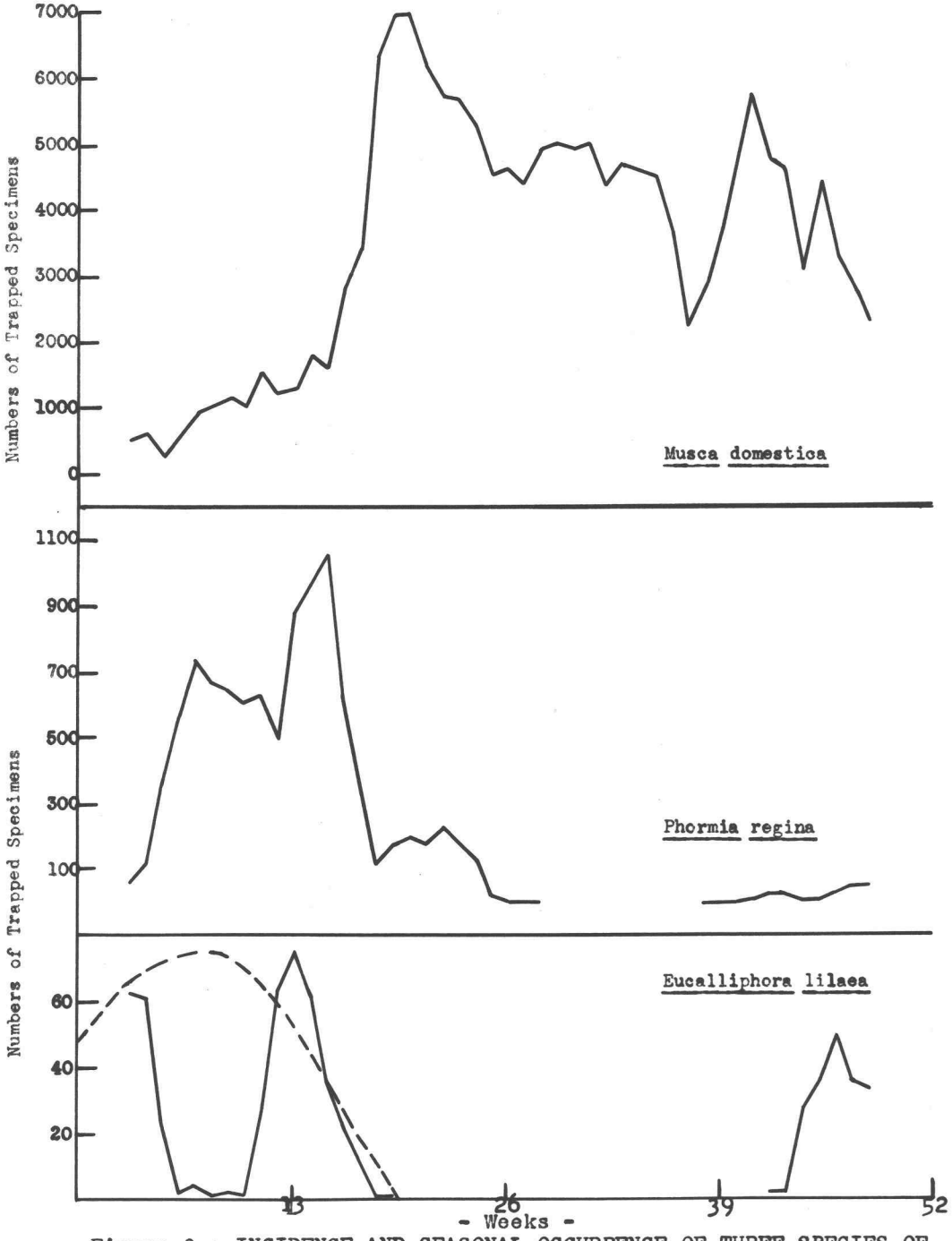


Figure 3. INCIDENCE AND SEASONAL OCCURRENCE OF THREE SPECIES OF FLIES TRAPPED AT PHOENIX, ARIZONA IN 1950

observed: (1) flies that were prevalent the year round, (2) flies somewhat restricted in their seasonal prevalence (i.e. of most frequent occurrence in spring and fall, or late summer and fall), and (3) those restricted to one season of the year. Of the above group Musca domestica is illustrative of the first type, and Phormia regina of the second type. Eucalliphora lilaea, since its occurrence was limited to the winter season, is considered illustrative of the third type.

Figure 3 illustrates two important points. First, by comparing the numbers of Musca domestica (and the weeks of the year when they were trapped) with Figure 2, it may be noted that the two graphs are roughly comparable. Thus, the seasonal occurrence and incidence of the housefly is very indicative of total fly indices in the area. Secondly, it may be noted that, although Phormia regina is exceeded in numerical prevalence by M. domestica, its initial peak occurs earlier in the year, and the peak prevalence of Eucalliphora lilaea precedes that of Phormia. It is significant that both Phormia and Eucalliphora are absent during the warm months of the year. Usually Phormia appears in larger numbers in late fall and Eucalliphora might better be represented by the dotted line as shown. Although Figure 2 represents the trap data for only one year, it may be considered as fairly representative of the sequence of initial peak prevalence and for the relative abundance of these three species in the area.

Objectives of the study

With reference to Figure 3, the following questions might be asked: Although houseflies are reputedly rapid in their development, why are their peak populations preceded in the spring by more seasonally-restricted forms? Why are certain species restricted in their prevalence to the winter season? How do these species survive during adverse conditions? These questions, and the foregoing discussion of the bimodal curve effect of total fly populations, lead to a formulation of the objectives of the study, as follows: to obtain, by a study of representative species, a better understanding of (1) the factors which contribute to the year-round prevalence and predominance of the housefly in a given area, (2) what factors may account for initial peaks of housefly populations occurring later in the year than more seasonally-restricted forms, and (3) what factors serve to limit the occurrence of certain seasonally-restricted types.

EXPERIMENTAL MATERIALS AND METHODS

Methods used in simulated field rearings

The field research building was located on a desert tract of land adjoining the Phoenix Airport. Part of this small building was partitioned off for use as a rearing room. This room measured eight by ten feet. The panel of the door was removed and replaced with screen. A window was left open at all times.

The rearing room was somewhat cooler in summer and warmer in winter than outdoor shade temperatures. During summer it was necessary to provide forced ventilation, since adult flies rapidly succumb at temperatures in excess of 105°F. while under confinement. Artificial heat maintained in the adjoining office during winter resulted in partial loss of this heat through the celotex partition into the rearing room.

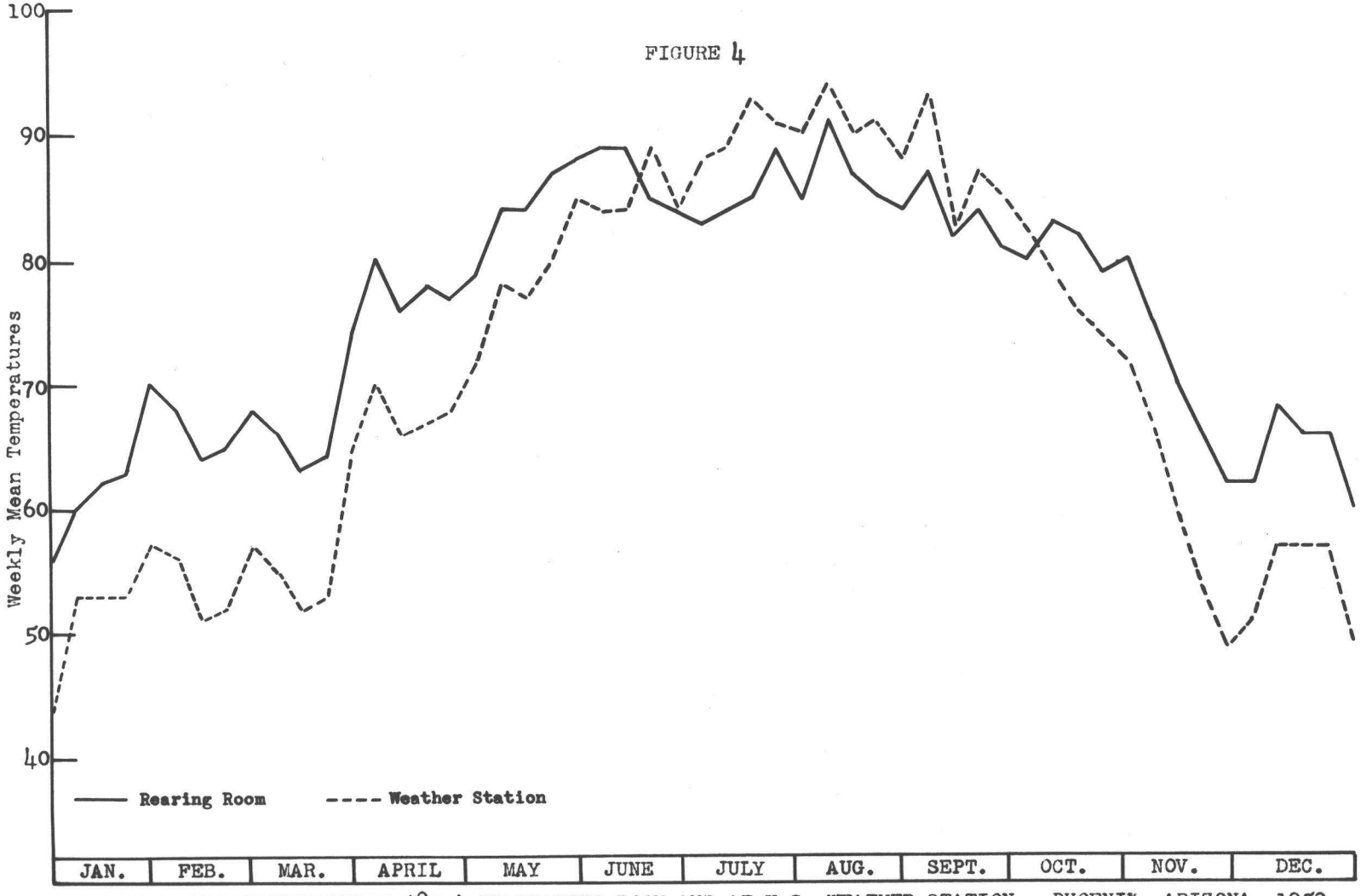
A rearing set-up of this type was the closest approximation to natural conditions as practicable in the field situation.[1] A hygro-thermograph[2] provided a continuous record of both temperature and relative humidity. Differences in maximum and minimum temperatures within given 24-hour periods varied from 19°F. in August to as much as 40°F. in January. Comparison of weekly mean temperatures in the rearing room with weekly mean outdoor temperatures is shown in Figure 4. Relative humidity data are not shown. These data are hardly applicable, since adult flies were provided with a constant supply of water and the media were kept sufficiently moist at all times.

Rearing cages were constructed from gallon-size ice cream cartons. The bottom of the carton was removed and a circular disc cut out leaving a one-inch rim. This disc was discarded. Plastic screen was substituted for the discarded central disc

[1] In tables and graphs, it is convenient to designate these rearings as "field" rearings as apart from the laboratory rearings conducted under constant temperature conditions at Oregon State College.

[2] Model 594, Bendix Aviation Corporation, Baltimore, Maryland

FIGURE 4



WEEKLY MEAN TEMPERATURES (°F.) IN REARING ROOM AND AT U.S. WEATHER STATION - PHOENIX, ARIZONA 1952

and fastened by staples to the one-inch rim. The cardboard bottom was then replaced. The carton, then inverted, served as a rearing cage with a screened top. Approximately one-quarter inch layer of sand was placed in the lid, which served as the removable bottom of the cage.

Colonies were started, for any given species, by hand capture or trapping in the field. Transparent plastic tubes with removable screw caps were useful in collecting gravid females. When microscopic examination was necessary in order to make positive species determination, the flies were anesthesized with carbon dioxide. After identification, one or more females were placed in rearing cages and allowed to oviposit.

Fish scraps were used as rearing media. A half-pint ice cream carton filled with fish was used to provision each cage at the time of introducing the gravid female flies. Each cage was provided with two or more sugar cubes. A metal salve box filled with water-soaked cellucotton was also placed on the floor of the cage. When necessary, additional amounts of water were pipetted through the screened top so that the cellucotton was moist at all times.

When eggs were first observed on the media, the media were transferred to another cage. In this way, the media were not re-infested by subsequent ovipositions and definite oviposition dates could be established. Only sugar and water remained for the adults in the cage where oviposition occurred. Longevity and

sex-ratio data were obtained by observations on these sustained adults.

In the cages containing infested media, mature larvae sought the sand layers in the bottom of the cages as a site for pupation. After pupation, media were removed and discarded. Upon emergence of adults, fresh media were provided until oviposition occurred. After ovipositiom, media were transferred to another cage and adults sustained on sugar and water. Thus, the procedure was repeated for each successively-reared generation of flies.

Screened, eighteen-inch square holding cages were used to house two or more rearing cages each. These holding cages provided protection from accidental contamination which might result from wild flies gaining access to the rearing room and dropping eggs or larvae into the rearing cages.

Methods used in laboratory rearings

The laboratory rearings were conducted at the Entomology Farm at Oregon State College during 1953 and 1954. For these rearings, constant temperature cabinets were used. These cabinets were constructed from used iceboxes purchased from war surplus stock. Constant temperatures were maintained by the use of a mercury thermoregulator[3] sensitive to 0.1°F. The thermoregulator was wired into a circuit with a relay, a small

[3] Manufactured by Julien P. Friez and Sons, Incorporated, Baltimore, Maryland. Available from Central Scientific Company, Chicago.

household type electric fan and three light bulb sockets (Figure 5). Three 60-watt light bulbs provided the source of heat. The fan was mounted on one side of the upper compartment and connected so as to run continuously. This prevented layering of air within the cabinet.

The constant temperature rearings were conducted in essentially the same manner as described for the simulated field rearings, except that breeding colonies were maintained for the purpose of providing eggs. Figure 6 shows one rearing carton, constructed from a gallon-size ice cream carton, tilted so as to show the sand layer in the bottom, and supported by a half-pint size ice cream carton of the type used to contain the media. In the lower compartment is shown a holding cage, converted from a top section of an attached-bait pan fly trap. The cone has been thrust out, and the cone opening sealed. The top has been removed, and replaced by a sleeve. A wooden cleat (not shown in the picture) was nailed to the bottom of the cage to prevent it rolling about on the floor of the cabinet. These small holding cages were used for maintaining breeding colonies of adult flies.

Both Corvallis and Phoenix strains[4,5] of Musca domestica, Phormia regina and Eucalliphora lilaea were used. Each rearing

[4] The term "strain" as used in this paper does not necessarily connote morphological or physiological differences, but is convenient terminology to merely indicate the localities where the flies were obtained.

[5] Acknowledgement is due Mr. John Ludwig of Phoenix, Arizona, who sent pupae of the three species to the writer at Corvallis, Oregon. These pupae were used in initiating colonies.

Constant Temperature Cabinet

Figure 5

Constant Temperature Cabinet
with Rearing Equipment

Figure 6

trial was replicated four or six times at a minimum of five temperature settings.

RESULTS

Statistical Methods Used

Analysis of developmental rates is considered as fundamental to the objectives of this study. The statistical method employed is that of linear regression. The applications of that statistical method to this particular problem are briefly described as a preface to presentation of the results.

It appears to be quite well established that a linear relationship exists between certain ranges of temperatures and developmental periods of certain insects, when these developmental periods are expressed as reciprocal values of time. The literature on this particular subject is quite extensive, and will not be reviewed at this point. West (56, pp.199-209) presents a good review of the literature, with special reference to developmental rates of houseflies. However, the statistical methods used in this study are not described by West, but are included in textbooks by Snedecor (52, pp. 103-137) and Dixon and Massey (13, pp.153-179).

If temperature (the independent variable) is designated as x, and reciprocal values of time in days (the dependent variable) is designated as y, a regression function can be derived which gives the relation between x and y. If the regression of y on

x is linear, the means of the arrays of y lie on a straight plane. The regression coefficient (b) which indicates the slope of the plane is an unbiased estimate of beta (the population regression coefficient). If deviations from linearity are statistically insignificant, analysis of covariance may be used in comparison of samples. This procedure consists of the following steps:

1. Test of hypothesis that the regression function of y on x is linear.
   a. Derivation of the sample regression coefficient (b)
   b. Derivation of the correlation coefficient (r)
2. Test of hypothesis that two or more beta values are equal.
3. Test of hypothesis that the adjusted means of two or more populations are equal.

Step 1 of the above procedure is illustrated in Tables 4a and 4b. Step 2 of the above procedure is illustrated in Table 15a. Calculations are somewhat involved in the third step of the procedure and only the end-points of these calculations are shown. Table 15b illustrates this third step in the procedure.

All of the tests for linearity follow the same pattern. Calculations involving the simulated field rearings for Musca are included in the text. Calculations involved in subsequent tests for linearity are reduced to show only the critical items used in the tests of hypotheses, and the b and r values. These tables and other tables showing statistical procedure are in the appendix. Graphs which summarize the developmental rates for each species are included with the text.

Musca domestica: Developmental rates at variable temperatures

Table 1 shows the numbers of both sexes of *M. domestica* reared under simulated field conditions at various mean temperatures. Unless otherwise stated, temperature readings are in Fahrenheit. The derivation of these mean temperatures is discussed in some detail below.

Table 2 shows the actual rearing data for the rearings given in Table 1. Under the conditions of the experiment, the termination of the egg stage and initiation of the larval stage were practically indistinguishable. These periods are combined and indicated as "egg-plus-larval period." "Half or more pupated" was the criterion used for determining the end of the larval stage and the beginning of the pupal period. Likewise, "half or more emerged" was the criterion used in designating the end of the pupal period or emergence of the adults. For any given period, average maximum temperatures were derived by totalling the highest daily readings from the hygro-thermograph charts and dividing by the numbers of observations. Average minimum temperatures were derived by totalling the lowest daily readings and dividing by the numbers of observations. Mean temperatures were derived by totalling all maximum and minimum daily readings, and dividing by the number of observations. These calculations were carried to two decimal places.

It may be noted in Table 3 that mean temperature values were associated with unequal numbers of observations. For example,

TABLE 1

Musca domestica - Field Rearings

Mean Temperature	Numbers of Pupae	Numbers of adults reared		
		Male	Female	Total
91	400	211	150	361
88	1035	465	469	934
85	1640	753	702	1455
82	374	180	182	362
79	115	47	60	107
76	621	310	287	606
67	752	357	384	741
64	313	138	122	260
61	326	158	168	326
Total	5576	2628	2524	5152

TABLE 2

Field Rearing Data for Musca domestica

Colony and Gen.	Egg plus larval per.	Ave. Max.	Ave. Min.	Mean	Days	Pupal Period	Ave. Max.	Ave. Min.	Mean	Days	Sum of Days	Mean Temp. Egg to Adult
M20 F-1	12/18/51-1/9/52	70.48	47.30	58.89	22	1/9/52-1/29/52	74.10	50.29	62.19	20	42	60.48
F-2	2/6/52-2/25/52	78.50	52.90	65.70	19	2/25/52-3/11/52	76.81	55.94	66.38	15	34	65.93
F-3	3/20/52-4/1/52	82.15	59.69	70.92	12	4/1/52-4/8/52	92.25	67.37	79.81	7	19	74.05
F-4	4/11/52-4/20/52	87.00	67.20	77.10	9	4/20/52-4/27/52	83.50	68.63	76.06	7	16	76.91
F-5	5/1/52-5/9/52	93.78	62.22	83.56	8	5/9/52-5/14/52	98.50	74.00	86.25	5	13	84.89
F-6	5/18/52-5/24/52	96.85	74.29	85.57	6	5/24/52-5/28/52	99.00	78.20	88.60	4	10	86.81
F-7	6/6/52-6/11/52	100.67	76.83	88.75	5	6/11/52-6/14/52	100.00	78.25	89.13	3	8	88.85
F-8	6/19/52-6/20/52	92.50	74.38	83.44	7	6/26/52-7/3/52	92.88	71.38	82.13	7	14	82.78
F-9	7/7/52-7/14/52	92.88	75.00	83.94	7	7/14/52-7/19/52	95.00	73.83	84.42	5	12	84.35
F-10	7/21/52-7/29/52	93.67	81.89	87.78	8	7/29/52-8/1/52	90.75	78.25	84.50	3	11	87.08
F-11	8/5/52-8/10/52	98.17	83.17	90.67	5	8/10/52-8/14/52	95.40	82.60	89.00	4	9	89.65
F-12	8/20/52-8/26/52	90.00	78.71	84.36	6	8/26/52-8/31/52	90.33	78.00	84.17	5	11	84.29
F-13	9/3/52-9/11/52	93.67	76.22	84.94	8	9/11/52-9/17/52	92.86	71.57	82.21	6	14	83.77
M1 F-1	11/7/51-11/17/51	78.00	61.75	69.88	10	11/17/51-11/26/51	74.50	58.00	66.25	9	19	68.18
M2 F-1	11/7/51-11/21/51	77.62	61.15	69.38	14	11/21/51-12/2/51	76.41	55.75	66.08	11	25	67.93
M23 F-1	1/3/52-1/23/52	70.67	48.48	59.62	20	1/23/52-2/8/52	81.87	52.60	67.23	16	36	63.00
F-2	2/25/52-3/9/52	78.00	55.64	66.82	13	3/9/52-3/24/52	72.43	55.19	63.81	15	28	65.21
F-3	4/1/52-4/7/52	93.43	66.86	80.14	6	4/7/52-4/13/52	85.29	67.00	76.14	6	12	78.14
F-4	4/19/52-4/28/52	83.30	68.70	76.00	9	4/28/52-5/2/52	85.80	67.20	76.50	4	13	76.15
F-5	5/8/52-5/13/52	97.17	73.33	85.25	5	5/13/52-5/18/52	94.00	71.83	82.92	5	10	84.09
F-6	5/23/52-5/29/52	98.29	77.29	87.79	6	5/29/52-6/1/52	97.50	77.75	87.63	3	9	87.74
F-7	6/7/52-6/13/52	100.29	77.00	88.64	6	6/13/52-6/17/52	102.20	78.80	90.50	4	10	89.38
F-8	6/24/52-6/29/52	93.33	75.50	84.42	5	6/29/52-7/5/52	92.14	73.14	82.64	6	11	83.45
F-9	7/12/52-7/17/52	92.00	71.83	81.92	5	7/17/52-7/22/52	97.33	80.83	89.08	5	10	85.50
F-10	7/25/52-7/30/52	91.33	80.00	85.67	5	7/30/52-8/2/52	92.75	77.50	85.13	3	8	85.47
F-11	8/14/52-8/19/52	91.33	80.17	85.75	5	8/19/52-8/23/52	91.80	79.00	85.40	4	9	85.60
F-12	9/4/52-9/9/52	96.00	77.17	86.58	5	9/9/52-9/14/52	91.83	70.17	81.00	5	10	83.79
F-13	10/9/52-10/17/52	91.00	70.67	80.83	8	10/17/52-10/25/52	92.56	67.88	80.22	8	16	80.53

TABLE 3

Distribution of Developmental-Time Periods (Days) for *Musca domestica* Field Rearings at Various Mean Temperatures

Temperature Interval	Midpoint of Interval	Developmental Periods In Days		
		Egg to adult	Pupal	Egg-plus-larval
-59.50-62.49	61	42	20	22,20
62.50-65.49	64	36,28	15	
65.50-68.49	67	34,19,25	15,9,11,16	19,13
68.50-71.49	70			12,10,14
71.50-74.49	73			
74.50-77.49	76	19,16,13	7,6,4	9,9
77.50-80.49	79	12	7,8	6,8
80.50-83.49	82	11,16,14	6,7,5,6,5	7,5
83.50-86.49	85	13,14,12,11,10,10,8,9,10	5,5,3,5,3,4	8,6,7,6,5,8,5,5,5
86.50-89.49	88	10,11,9,10,8	4,3,4,3,5	5,8,6,6,5
89.50-92.49	91	9	4	5

TABLE 4a

Musca domestica - Field Rearings - Egg to adult

91	88	85	82	79	76	67	64	61
(9)111	(10)100	(13)77	(11)91	(12)83	(19)53	(34)29	(36)28	(42)24
	(11)91	(14)71	(16)63		(16)63	(19)53	(28)36	
	(9)111	(12)83	(14)71		(13)77	(25)40		
	(10)100	(11)91						
	(8)125	(10)100						
		(10)100						
		(8)125						
		(9)111						
		(10)100						

T	111	527	858	225	83	193	122	64	24
T^2	12321	277729	736164	50625	6889	37249	14884	4096	576
N	1	5	9	3	1	3	3	2	1
T^2/N	12321	55545.8000	81796.0000	16875.0000	6889.00	12416.3333	4961.3333	2048.00	576.00

N	28						N	28
$\sum x$	2239						$\sum y$	2207
$\bar{x}$	79.9643						$\bar{y}$	78.8214
$(\sum x)^2$	5013121	$(\sum x)(\sum y)$	4941473				$(\sum y)^2$	4870849
$(\sum x)^2/N$	179040.0357	$(\sum x)(\sum y)/N$	176481.1785				$(\sum y)^2/N$	173958.8928
$\sum x^2$	181147.0000	$\sum xy$	182816.0000				$\sum y^2$	197427.0000
S.S.x	2106.9643	SP	6334.8215				S.S.y	23468.1072

$b = 3.0066$

Regression S.S. = 19046.3424

Residual S.S. = 4421.7648

$r^2 = .811584$

$r = .901$

TABLE 4b

ANALYSIS OF VARIANCE CALCULATIONS

Experiment: Musca domestica - Field Rearings
Egg to adult Periods

Preliminary Calculations

(1) Source of Variation	(2) Total of Squares	(3) No. of items Squared	(4) Observations per Squared Item	(5) Total of Squares per Observation (2)÷(4)
Correction	4870849	1	28	173,958.8928
Column	$\Sigma T^2/N$	-	-	193,428.4666
Individual Observations	197427.0000	28	1	197427.0000

ANALYSIS OF VARIANCE

Variation Due to:	Sum of Squares	Degrees of Freedom	Mean Square	F	Remarks
Column	19,469.5738	8			
Regression	19046.3424	1)			
Deviations from Regression	423.2314	7)	60.4616	.30	Accept hypothesis F is <2.54 at 7 and 19 d.f.
Error	3998.5334	19	210.4491		

one colony was reared at a mean temperature of 61°F., while three colonies were reared at 76°, and nine colonies at 85°. This situation is not the most desirable, but it can hardly be avoided when rearings are purposely conducted in such a way as to simulate natural conditions as closely as possible. There is a tendency for more colonies to complete their development at more optimum temperatures. The calculations are more difficult and time-consuming with unequal numbers of observations. However, the values derived are reliable and can be used as a basis for comparison with values obtained from other rearings, regardless of whether the observations are equal or unequal for values of x.

Table 4a shows the developmental rate derived for egg to adult periods of Musca domestica reared under simulated field conditions. This rate is expressed as the regression coefficient, 3.0066. The x values are obtained from Table 3. The y values are arranged with respect to x, and are derived by dividing each of the parenthetical values (also shown in Table 3) into 1, and multiplying by 1000.[6]

Developmental rates were also derived for the egg-plus-larval and pupal periods of Musca reared under simulated field conditions. These increments of the egg to adult period are shown in Table 2. The distribution of developmental-time periods for both pupal and

[6]Multiplying by 1000 eliminates the decimal points in the calculation, and yields values for y which are not too large for convenient manipulation with a calculating machine.

egg-plus-larval periods are given in Table 3. These tables are self-explanatory. The tests of hypothesis indicate that a linear relationship exists between developmental-time and temperature for egg-plus-larval and pupal periods as well as for egg to adult period (Tables 5,6).

Musca domestica: Developmental rates at constant temperatures

Rearing trials were run at each of six temperature settings (88°, 84°, 80°, 75°, 70° and 65°F.) for both Corvallis and Phoenix strains of M. domestica (Tables 7 and 11). Developmental rates derived for egg-plus-larval, pupal and egg to adult periods are shown in Tables 8-10 and Tables 12-14.

Musca domestica: comparison of developmental rates at variable and constant temperatures

Egg to adult periods will be considered first. Flies indigenous to the area were utilized in the simulated field rearings. In the laboratory rearings, both Corvallis and Phoenix flies were used. Essentially, do these constitute samples from only one population, or as many as three populations?

Reference is made to the procedure as outlined on page 17. Applying step 2 in this procedure, one may test the hypothesis that the regression coefficients for the three sets of rearings are equal. Calculations for testing this hypothesis are shown in Table 15a. Acceptance of this hypothesis indicates that regression lines for the three populations are parallel.

TABLE 7

Musca domestica - Laboratory Rearings - Corvallis strain

Colony	Developmental Periods In Days: Egg plus larval	Pupal	Egg to adult	Temperature
MC-7	15	13	28	65
MC-9	13	14	27	65
MC-12	13	13	26	65
MC-13	11	13	24	65
MC-15	12	16	28	65
MC-18	12	13	25	65
MC-25	11	9	20	70
MC-29	9	9	18	70
MC-32	7	11	18	70
MC-34	8	11	19	70
MC-35	12	9	21	70
MC-39	9	10	19	70
MC-3	7	8	15	75
MC-4	7	8	15	75
MC-14	6	7	13	75
MC-20	5	8	13	75
MC-22	5	9	14	75
MC-11	7	6	13	75
MC-26	5	7	12	80
MC-28	5	7	12	80
MC-30	6	4	10	80
MC-43	5	5	10	80
MC-45	6	5	11	80
MC-47	5	5	10	80
MC-1	5	4	9	84
MC-5	5	5	10	84
MC-6	5	5	10	84
MC-8	5	6	11	84
MC-10	4	7	11	84
MC-19	4	6	10	84
MC-23	4	4	8	88
MC-24	5	4	9	88
MC-27	4	5	9	88
MC-31	5	5	10	88
MC-33	4	4	8	88
MC-37	4	6	10	88

TABLE 11

Musca domestica - Phoenix strain - Laboratory Rearings

Colony	Developmental Periods In Days: Egg plus larval	Pupal	Egg to Adult	Temperature
MP-5	12	16	28	65
MP-6	15	15	30	65
MP-7	16	18	29	65
MP-14	17	10	27	65
MP-15	18	10	28	65
MP-17	17	10	27	65
MP-20	10	8	18	70
MP-23	11	9	20	70
MP-26	9	12	21	70
MP-32	9	12	21	70
MP-34	8	11	19	70
MP-37	10	10	20	70
MP-11	7	8	15	75
MP-12	6	8	14	75
MP-13	6	7	13	75
MP-16	8	6	14	75
MP-39	7	6	13	75
MP-40	6	9	15	75
MP-21	5	5	10	80
MP-24	5	6	11	80
MP-27	5	6	11	80
MP-29	5	5	10	80
MP-30	6	6	12	80
MP-35	6	5	11	80
MP-1	5	4	9	84
MP-2	5	5	10	84
MP-3	6	4	10	84
MP-4	4	6	10	84
MP-8	5	6	11	84
MP-9	5	6	11	84
MP-18	5	4	9	88
MP-19	4	4	8	88
MP-25	4	4	8	88
MP-28	4	5	9	88
MP-31	5	5	10	88
MP-36	5	5	10	88

Applying step 3 in the procedure (page 17), one may test the hypothesis that the adjusted means of the three populations are equal. Rejection of this hypothesis (Table 15b) (F is greater than 3.09 at 2 and 96 degrees of freedom) indicates that the regression lines for the three populations are not identical. From inspection of the data, it appears as if the character of the developmental rates for field rearings constitute the main cause for rejection of the hypothesis. This observation is confirmed by the result of testing the hypothesis that the adjusted means for the two strains, when reared at constant temperatures, are equal. These calculations are shown in Table 16b. One may accept this hypothesis at the 5% level of significance (F is less than 3.98 at one and 69 degrees of freedom).

Thus, since all developmental rates for both strains of Musca reared at constant temperatures constitute, essentially, one population, the two b values may be pooled in deriving $\bar{y}x$. Table 17 shows the calculations used in preparing the graphs shown in Figures 7, 8 and 9. These figures will serve as points of reference for reviewing the temperature-developmental time relationships for Musca domestica:

(1) The developmental rates for the egg to adult periods and the increments of this pre-imaginal period show conformation to linearity, regardless of whether temperatures are constant or

variable, throughout a temperature range of 65 to 88°F.[7]

(2) Simulated field rearings are characterized by greater variation among replications than are the laboratory rearings. Conformations to linearity, regardless of the nature of the temperatures are: egg to adult > egg-plus-larval periods > pupal periods.

(3) Statistically, the regression lines in Figure 7 are shown to be parallel, but not identical. They represent two distinct "populations" - development for the overall, egg to adult periods proceeding at a faster rate under constant temperature conditions than under variable temperature conditions.

(4) The differences in developmental rates between Corvallis and Phoenix strains of flies, when reared under constant temperature conditions, were statistically insignificant.

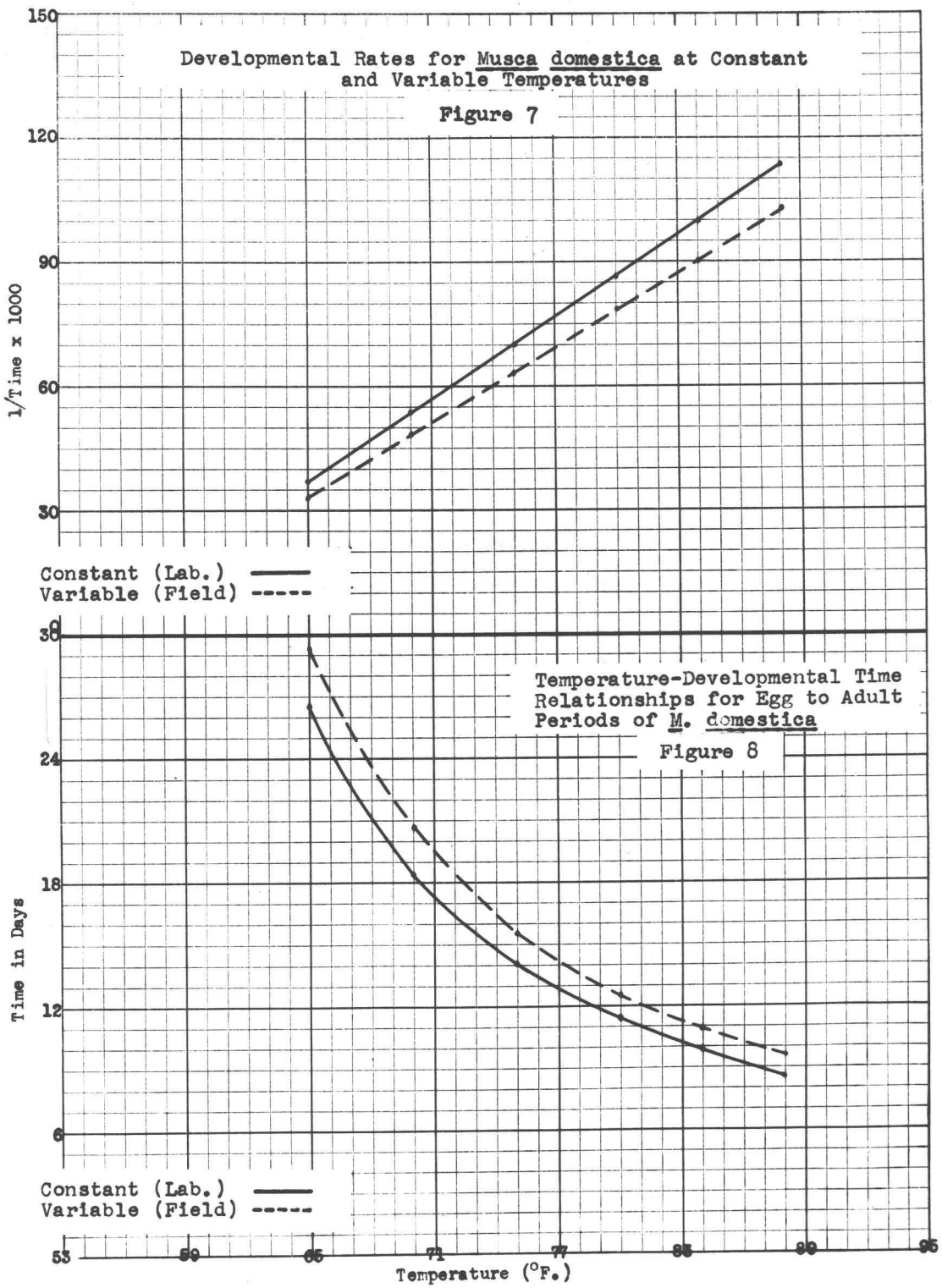
Musca domestica: other biological factors

The subject of housefly biology is quite extensive. Only those topics which are immediately applicable to this problem will be mentioned. Developmental rates constitute an important - but only one - line of evidence in an attempt to explain predominance and seasonal prevalence of houseflies in a given area. Their utilization of various production media is also of considerable

[7] Actually this linear relationship under constant temperature conditions applies to a more extended range (through 95°F). This item will be discussed later. However, the b values are essentially unchanged. The more restricted range serves as a better basis for comparison with field rearings at this point.

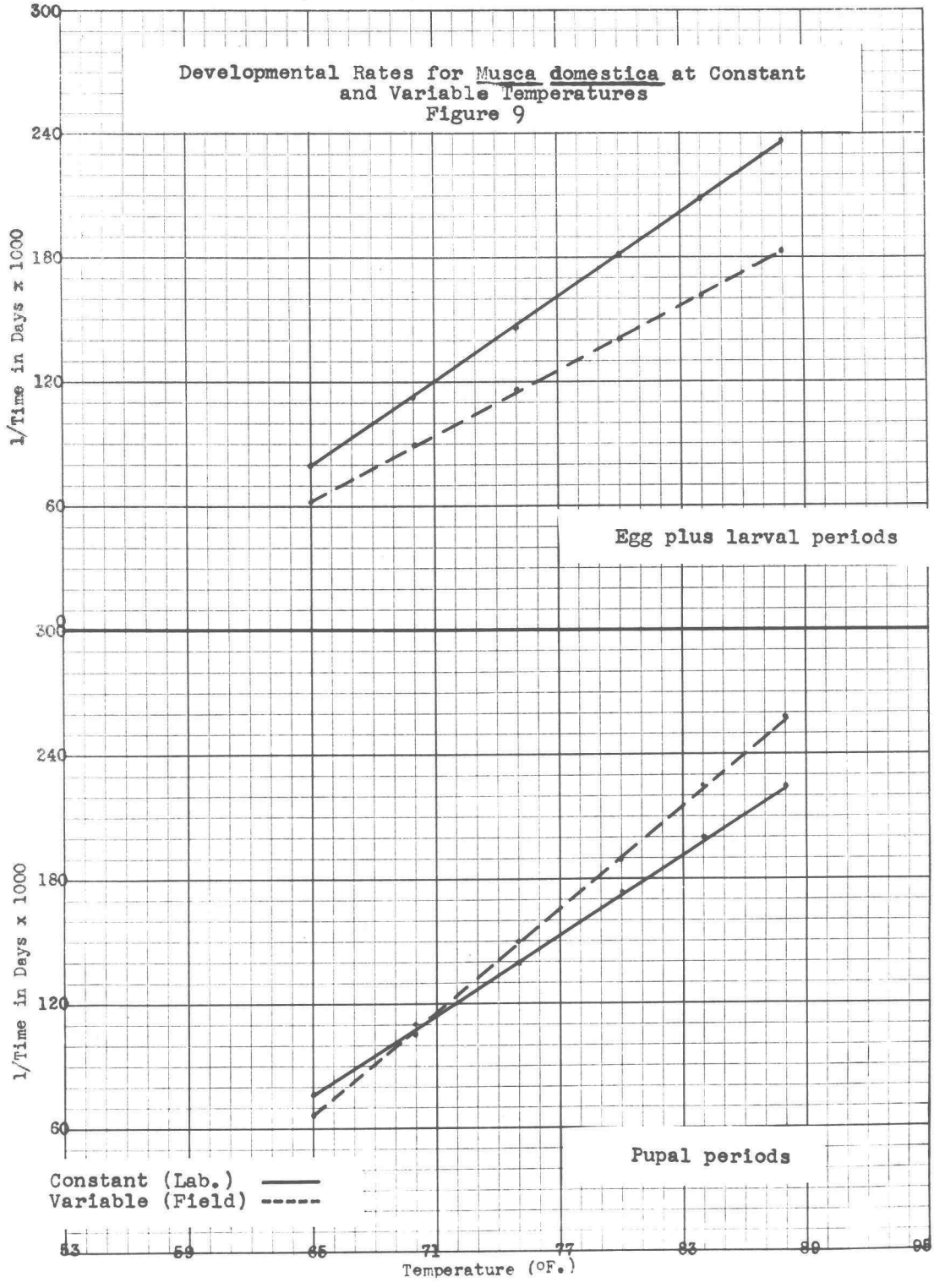
Developmental Rates for Musca domestica at Constant and Variable Temperatures

Figure 7



Temperature-Developmental Time Relationships for Egg to Adult Periods of M. domestica

Figure 8


Developmental Rates for Musca domestica at Constant and Variable Temperatures
Figure 9
1/Time in Days x 1000
300
240
180
120
60
Egg plus larval periods
300
240
180
120
60
Pupal periods
Constant (Lab.)
Variable (Field)
53
59
65
71
77
83
89
95
Temperature (°F.)

importance in this regard.

A fly breeding survey was conducted as an independent study for four continuous seasons in the Phoenix area. The results of this survey have been reported (51) in a series of three papers. Briefly, the findings that pertain to Musca domestica are applicable here. In more than 2240 positive samples examined, Musca larvae were present in 1149. On a seasonal breakdown, Musca was most predominant in larval samples during summer. However, it exceeded, even in winter, the highest incidence of any species recovered regardless of season. Most striking was the versatility of this species in utilization of various kinds of media. Horse excrement (reputedly the preferred breeding medium for houseflies) accounted for only 122 of the 1149 positive samples containing Musca larvae. This was exceeded in incidence of housefly-infested substrates by chicken excrement and scattered and contained garbage. Larvae of M. domestica were recovered from more than 50 per cent of the samples and from 19 of the 21 different classifications of media. Of 79 samples of infested grass clippings, 58 were positive for Musca; of 49 samples of infested coffee grounds, 26 were positive for Musca; and of 43 samples of infested melon, Musca were positive in 42 of these. Haines, (22, p.939) in his study of media utilized by flies in urban communities in southern Georgia, also emphasizes the versatility of M. domestica in its utilization of a wide range of breeding media, far exceeding all other fly species in this respect.

The literature regarding pre-oviposition periods contains conflicting accounts. Glaser (17, p.411) reports the pre-oviposition period as extending from 11 to 24 days, not considering temperature as a significant factor in shortening its duration. Bishopp, Dove and Parman (4, p.58) state that the length of the pre-oviposition period for houseflies may vary from four days at a temperature of 87°F. to 20 days at a temperature of 68°F. Larsen and Thomsen (23, p.32) constructed a regression curve, based on an approximation of the developmental rate for this period. They report a range of from 16.62 days at about 13°C. to 1.82 days at 34.8°C.

Pre-oviposition periods observed in this study varied from three to nine days. For flies maintained at about 80°F. in the Entomology Rearing Room at Oregon State College, four days is considered the minimum pre-oviposition period.

In nature, such substrates as extensive piles of animal excrement may require searching for several minutes before eggs can be found. Where eggs are located, they are often present in tremendous numbers, yet to human sense discrimination that particular micro-environment is no different than any of the surrounding area. Failure of caged flies to oviposit may present a puzzling problem at times and lead to actual loss of colonies. Erratic ovipositional response suggests that certain aspects of housefly behavior may be one of the indeterminate variables which mislead the investigator in relating pre-oviposition period to one environmental factor, such as temperature.

Four flight range tests were conducted in the Phoenix area. The results of these investigations were reported in three papers (44, 48, 45). Of these three papers the one dealing with pattern of movement of Musca domestica is probably the most instructive. The writers (45) used both dyes and radioactive phosphorus as tagging agents in this study. The findings indicate that in a homogenous area, the secondary as well as primary pattern of dispersal follows a radial design. The findings support previous observations that the housefly is essentially an insect of migrating habits, and the significance of this factor in disease transmission is emphasized.

During the warm summer months, fly activity diminished by 11 a.m. (or at about 100°F. shade temperatures) and activity was not resumed until late in the evening. Flies would rest during the warmest part of the day in protected habitats, such as in shade trees and around evaporative coolers. Interestingly, there appears to be a difference in temperature threshold for adult activity between Corvallis and Phoenix flies. With increasing temperatures, flies of the Corvallis strain became active at about 65°F. while Phoenix strain flies started active movements at about 70°F. Bucher, Cameron and Wilkes (7, p.61) found that temperatures at which houseflies became active, and at which they commence feeding are almost the same. These authors state that the temperature limits for feeding are apparently very near the limits for general activity.

"How long do flies live?" is a question that laymen frequently ask. Flies sustained under variable temperatures lived a maximum period of 57 days. The mean period required for 100% mortality of a colony sustained under variable temperatures was 43.0 days. Dove (15, p.537) found that houseflies maintained at temperatures below 60°F. were able to survive for as long as 91 days. Caged flies at rearing room temperatures of 80°F. may live for six weeks, but the optimum period for egg production is 30 days or less.

Estimates on fecundity of houseflies are also variable. According to James (31, p. 141) a single female may produce 120 to 150 eggs in a batch and may deposit from five or six to 20 batches in her lifetime. Hewitt (27, p.114) states that a single fly may deposit from 100 to 150 eggs in a single batch and that during its lifetime it may deposit from four to six batches. Howard (29, p.39) places the figure at 120 eggs per batch, and four batches of eggs produced during the life span of the female. Howard's estimates are very close to those obtained from colonies maintained in the Entomology Rearing Room at Oregon State College. Over a period of 16 weeks, four generations of caged flies produced an estimated average of 110 eggs per female per week, or 440 eggs per female during adult life.

Howard (29, p.38) calculated that 5,598,720,000 flies could be produced from a single mating, between April 15 and Sept. 10 in the latitude of Washington, D. C. His calculations are based upon the assumption that a gravid female lays 120 eggs, a 1:1 sex

ratio, and a time interval of 20 days between generations. However, this figure is only the number of adults represented by the seventh generation. For the field rearings in Phoenix, the mean interval between generations was 19.3 days. Since fly production extends in that area through 12 months of the year, the number of annual generations may be estimated at 360/20 or 18. Since the increase is geometric, the number represented by the 18th generation would be enormous.

Phormia regina: Developmental rates at variable temperatures

Phormia regina, the black blowfly, was reared at Phoenix under simulated field conditions during 1951 and 1952. The numbers of Phormia reared are shown in Table 18. The field rearing data for this species are shown in Table 19. Temperature intervals used in deriving midpoint values are the same as those used for Musca domestica. The breakdown for developmental periods at various mean temperatures is given in Table 20.

Developmental rates were derived for egg to adult, egg-plus-larval and pupal periods. Deviations from linearity were insignificant in each case. Tests for linearity with corresponding b and r values for these rearings are shown in Tables 21 to 23.

Phormia regina: Developmental rates at constant temperatures

For the constant temperature trials, rearings were conducted at each of six temperature settings (88°, 84°, 80°, 75°, 70°, and 65°F.). Six replicated trials at each temperature setting were run

with the Corvallis strain Table 24). Four replicated trials at each temperature setting were run with the Phoenix strain Table 28).

Tests for linearity were run from the data obtained for egg to adult, egg-plus-larval and pupal periods of both strains. Deviations from linearity were insignificant in each case. The results of these laboratory rearings are given in Tables 25-27 and Tables 29-31.

Phormia regina: comparison of developmental rates at variable and constant temperatures

A wider discrepancy exists between developmental rates at constant and at variable temperatures than in the case of Musca domestica. However, differences in the regression coefficients (Table 32a)are shown to be insignificant (F value of 1.41 is less than 3.13 at 2 and 73 degrees of freedom). Acceptance of this hypothesis indicates that the regression lines for the three populations of Phormia are parallel.

Rejection of the hypothesis tested in Table 32b would indicate that the regression lines for the three populations are not identical. As in the case of Musca domestica, cause for rejection of the hypothesis is the slower developmental rate under variable temperatures. When simulated field rearings are deleted and only laboratory rearing trials are tested, the regression coefficients and the adjusted means are equal (Tables 33a and 33b) (F is less than 4.02). Since the developmental rates for

TABLE 18

Phormia regina - Field Rearings

Mean Temperature		Numbers of Pupae	Numbers of adults reared Male	Female	Total
67		909	425	407	832
73		186	81	86	167
79		854	377	391	768
82		335	145	149	294
85		1494	735	691	1426
88		847	359	410	769
	Total	4625	2122	2134	4256

TABLE 19

Field Rearing Data for *Phormia regina*

Colony	Gen.	Egg plus larval per.	Temperature (°F.) Ave. Max.	Ave. Min.	Mean	Days	Pupal Period	Temperature (°F.) Ave. Max.	Ave. Min.	Mean	Days	Sum of Days	Mean Temp. Egg to Adult
P-5	F-1	11/8/51-11/21/51	77.50	61.25	68.96	13	11/21/51-12/4/51	76.64	60.30	66.18	13	26	67.57
P-32	F-1	2/6/52-2/19/52	77.07	52.86	64.96	13	2/19/52-3/4/52	79.27	54.13	66.70	14	27	66.31
	F-2	3/26/52-4/3/52	88.78	64.11	76.44	8	4/3/52-4/9/52	91.71	67.71	79.71	6	14	77.87
	F-3	4/17/52-4/29/52	84.54	63.21	76.31	12	4/29/52-5/4/52	92.17	69.67	80.92	5	17	78.08
	F-4	5/12/52-5/18/52	95.00	71.86	83.43	6	5/18/52-5/22/52	95.40	74.40	84.90	4	10	84.41
	F-5	6/25/52-7/1/52	93.29	74.00	83.64	6	7/1/52-7/6/52	92.43	74.29	83.36	5	11	83.54
	F-6	7/13/52-7/19/52	94.14	73.29	83.71	6	7/19/52-7/25/52	96.43	83.00	89.71	6	12	86.58
	F-7	8/1/52-8/7/52	95.57	80.71	88.14	6	5/7/52-8/11/52	98.60	82.80	90.70	4	10	89.14
	F-8	8/15/52-8/22/52	91.13	79.25	85.18	7	8/22/52-8/26-52	89.60	78.60	84.10	4	11	84.75
	F-9	9/4/52-9/11/52	93.25	75.88	84.56	7	9/11/52-9/18/52	92.63	72.25	82.44	7	14	84.07
	F-10	9/24/52-10/3/52	89.20	71.30	80.25	9	10/3/52-10/8/52	91.83	69.00	80.41	5	14	80.40
	F-11	10/12/52-10/21/52	93.50	70.10	81.80	9	10/21/52-10/26/52	90.17	66.67	78.42	5	14	80.64
P-8	F-1	6/12/52-6/19/52	100.25	76.87	88.56	7	6/19/52-6/27/52	92.11	74.67	83.39	8	15	85.30
	F-2	7/3/52-7/9/52	92.29	78.57	85.13	6	7/9/52-7/15/52	92.86	72.86	82.86	6	12	84.15
	F-3	7/22/52-7/27/52	94.00	82.33	88.17	5	7/27/52-8/3/52	92.00	78.13	85.06	7	12	86.54
	F-4	8/7/52-8/13/52	97.00	82.57	89.79	6	8/13/52-8/18/52	91.50	80.33	85.92	5	11	88.18
	F-5	8/25-52-9/2/52	90.56	77.89	84.22	8	9/2/52-9/7/52	97.17	78.67	87.92	5	13	85.68
	F-6	9/15/52-9/21/52	90.29	76.86	83.57	6	9/21/52-10/1/52	88.36	73.18	80.77	10	16	81.88
	F-7	10/10/52-10/19/52	93.50	70.38	81.94	9	10/19/52-10/29-52	92.45	67.00	79.73	10	19	80.36
	F-8	11/7/52-11/16/52	79.70	61.70	70.70	9	11/16/52-12/1/52	77.19	56.38	66.79	15	24	68.25
P-7	F-1	11/9/51-11/18/51	75.88	61.50	68.69	9	11/18/51-12/3/51	77.50	56.38	66.94	15	24	67.59
	F-2	2/6/52-2/19/52	77.07	52.86	64.96	13	2/19/52-3/5/52	79.38	54.13	66.75	15	28	65.92
	F-3	3/17/52-3/31/52	80.40	58.87	69.63	14	3/31/52-4/9/52	91.40	66.90	79.15	9	23	73.31

TABLE 20

Distribution of Developmental-Time Periods (Days) for *Phormia regina* Field Rearings at Various Mean Temperatures

Temperature Interval	Midpoint of Interval	Developmental Periods In Days		
		Egg to Adult	Pupal	Egg plus larval
59.50-62.49	61			
62.50-65.49	64			13,13
65.50-68.49	67	26,27,28,24	13,14,15,15,15	
68.50-71.49	70			9,14,13,9
71.50-74.49	73	23		
74.50-77.49	76			8,12
77.50-80.49	79	14,17,14,19	6,5,5,10,9	9
80.50-83.49	82	14,16	5,5,7,10,8,6	6,9,9
83.50-86.49	85	10,11,11,14,13,15,12	4,4,7,5	6,6,7,7,8,6,6
86.50-89.49	88	12,10,12,11	5	6,5,7
89.50-92.49	91		6,4	6

TABLE 24

Phormia regina - Corvallis strain - Laboratory Rearings

Colony	Developmental Periods in Days			
	Egg plus larval	Pupal	Egg to Adult	Temperature
PC-2	14	10	24	65
PC-4	14	9	23	65
PC-5	15	8	23	65
PC-6	15	9	24	65
PC-11	12	12	24	65
PC-34	13	9	22	65
PC-21	10	8	18	70
PC-27	12	7	19	70
PC-32	9	8	17	70
PC-37	11	9	20	70
PC-38	10	9	19	70
PC-39	10	8	18	70
PC-7	6	8	14	75
PC-8	6	8	14	75
PC-10	6	8	14	75
PC-16	9	6	15	75
PC-17	7	6	13	75
PC-18	7	6	13	75
PC-22	5	6	11	80
PC-24	5	7	12	80
PC-26	6	7	13	80
PC-29	7	5	12	80
PC-35	6	5	11	80
PC-36	7	6	13	80
PC-3	5	6	11	84
PC-9	4	6	10	84
PC-13	5	4	9	84
PC-14	6	5	11	84
PC-15	5	5	10	84
PC-40	7	4	11	84
PC-19	4	5	9	88
PC-20	5	4	9	88
PC-23	5	6	11	88
PC-25	5	4	9	88
PC-30	6	4	10	88
PC-33	4	5	9	88

TABLE 28

Phormia regina - Phoenix strain - Laboratory Rearings

Colony	Developmental Periods in Days			
	Egg plus larval	Pupal	Egg to adult	Temperature
PP-3	14	10	24	65
PP-5	16	8	24	65
PP-7	15	10	25	65
PP-30	15	9	24	65
PP-13	8	7	15	70
PP-16	9	8	17	70
PP-24	12	7	19	70
PP-27	8	10	18	70
PP-1	7	5	12	75
PP-2	7	7	14	75
PP-6	8	6	14	75
PP-10	6	7	13	75
PP-14	5	5	10	80
PP-21	6	4	10	80
PP-23	5	5	10	80
PP-25	6	6	12	80
PP-4	6	4	10	84
PP-8	6	5	11	84
PP-9	5	5	10	84
PP-28	5	5	10	84
PP-11	6	4	10	88
PP-12	5	4	9	88
PP-17	5	6	11	88
PP-26	4	4	8	88

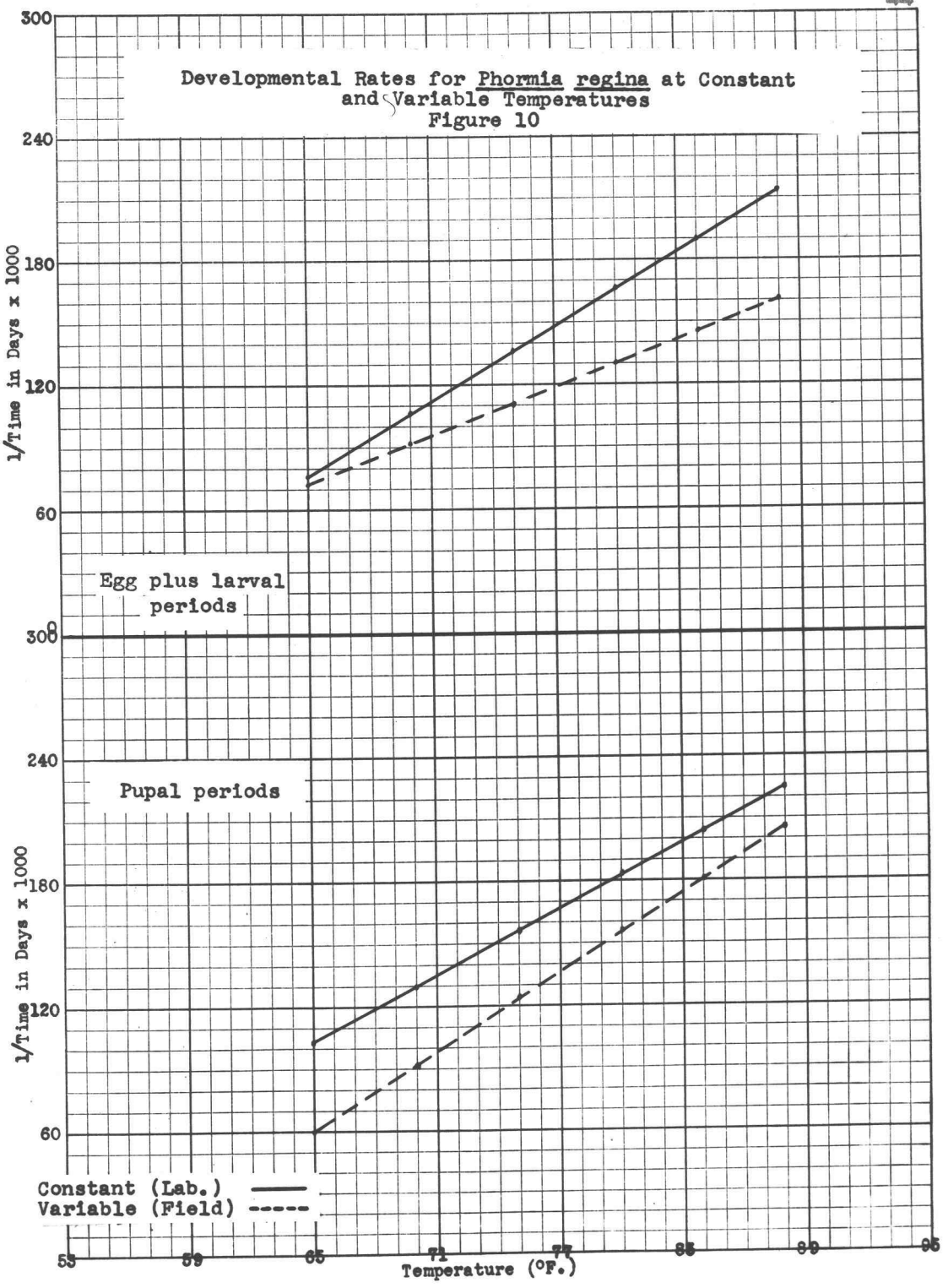
Corvallis and Phoenix strains, when reared under constant temperature conditions constitute, essentially, one population, pooled values for b, $\bar{y}$ and $\bar{x}$ may be used in deriving $\bar{yx}$ for use in constructing curves.

Values for $\bar{yx}$ at each of the six temperature settings used are given in Table 34 for both variable and constant temperature rearings. These values are plotted and shown in Figures 10, 11 and 12.

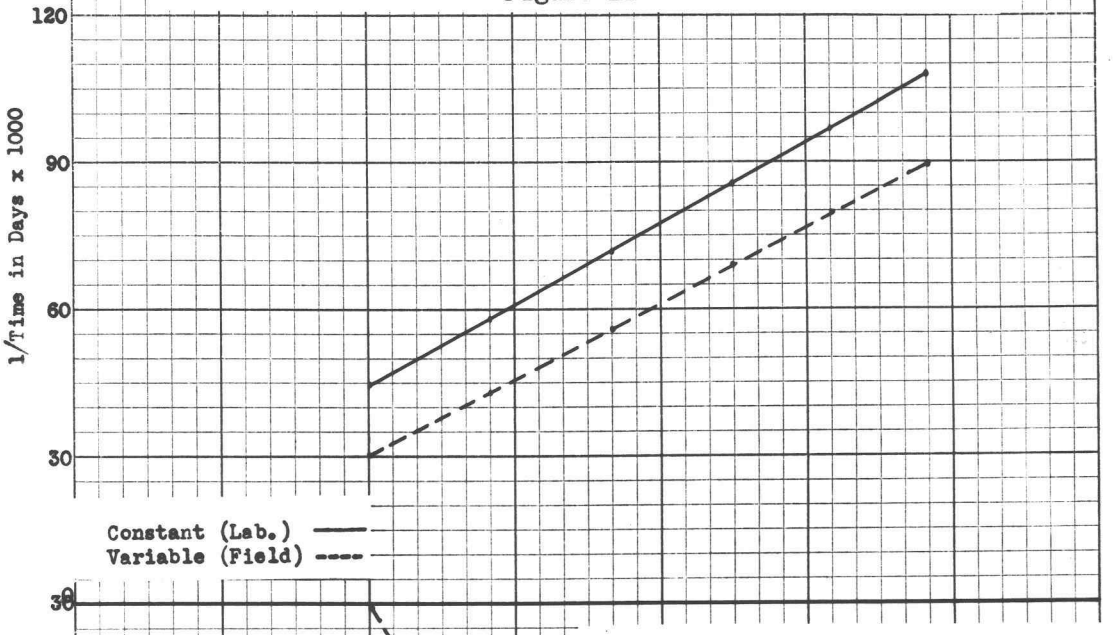
Essentially, the points listed (page 29) which summarize the temperature-developmental time relationships for Musca domestica are also applicable to Phormia regina. Effects of variable temperatures were especially retarding upon developmental rates of the egg and larval stages of Phormia. Reasons for differences in developmental rates under variable and constant temperatures for Musca as well as Phormia are discussed in a later section.

Phormia regina: other biological factors

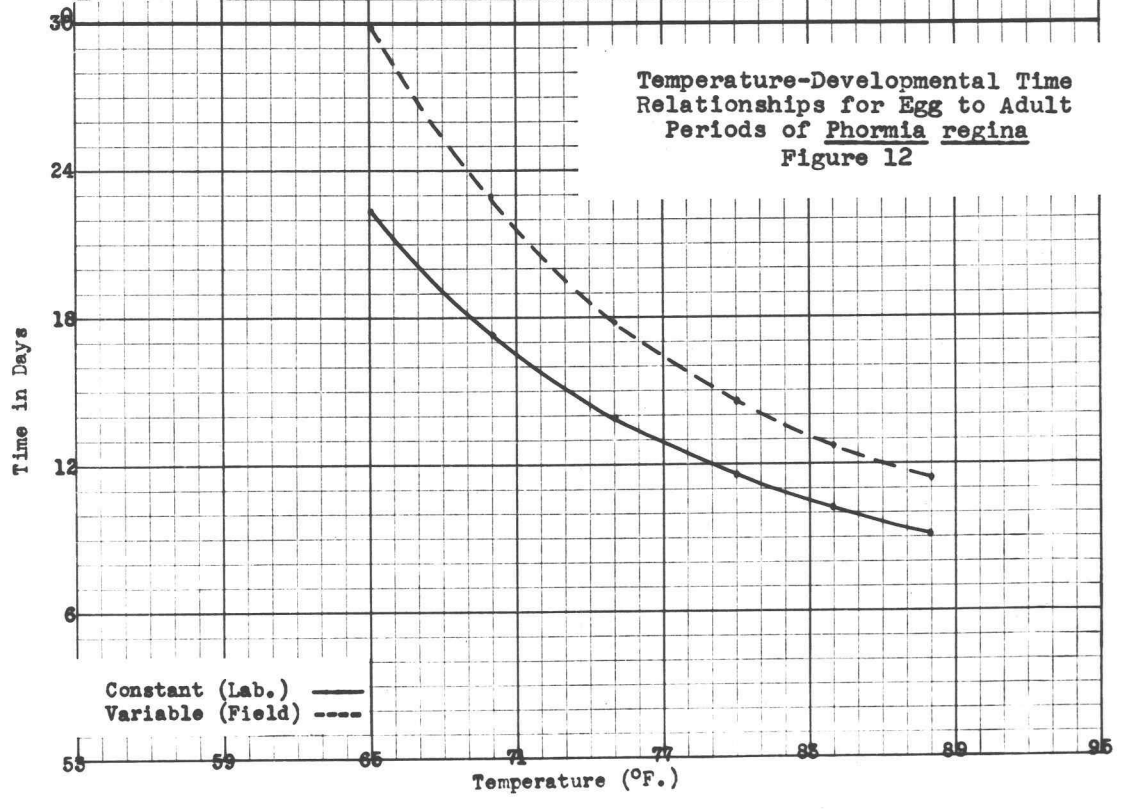
In comparison with the housefly, Phormia appears to be quite restricted in its utilization of various types of production media. In connection with the larval survey conducted in the Phoenix area, Phormia larvae were recovered from only three of the 21 different classifications of media (51). These three substrates were scattered garbage, contained garbage and animal carcasses. According to Hall (23, p.167) the larvae are normally saprophagous. Haines (22, p.937) found that in southern Georgia, 95% of Phormia


Developmental Rates for Phormia regina at Constant and Variable Temperatures
Figure 10
1/Time in Days x 1000
300
240
180
120
60
Egg plus larval periods
Pupal periods
Constant (Lab.)
Variable (Field)
55
59
65
71
77
83
89
95
Temperature (°F.)

Developmental Rates for Phormia regina at Constant and Variable Temperatures
Figure 11



Temperature-Developmental Time Relationships for Egg to Adult Periods of Phormia regina
Figure 12



infestations were from animal wastes, consisting of bones of cows and hogs, animal carcasses, entrails, fish remains, paunch manure and other packing house wastes. Animal wastes of this kind are not commonly available in most metropolitan areas. Under city conditions, apparently the best substitute for these high-protein wastes is garbage - especially if the garbage contains quantities of meat scraps. Of 65 collected samples positive for Phormia regina in Charleston, West Virginia, 40 were taken from contained garbage (47, p.249).

For the past year, Phormia regina has been successfully reared at Oregon State College on a synthetic medium. The medium and methods are those described by Hill, Bell and Chadwick (28, pp. 213-216) with two modifications: (1) 60 ml. of cholesterol suspension, containing 50 mg. of cholesterol is substituted for lanolin in the medium, and (2) sterile sawdust is added to the flasks containing media immediately after seeding with eggs. Cholesterol appears to satisfy nutritive requirements for the larvae as well as lanolin, and has the advantage of being easier to handle in the laboratory. However, larvae do not complete development in this synthetic medium as rapidly as in fish. At temperatures near a constant level of 80°F., an average of 9 days is required for completion of larval development with this medium, but only six days when fish is used.

Observed pre-oviposition periods of from four to 18 days are comparable with those reported by Bishopp (2, p.327) of from seven to 18 days.

Phormia regina is a strong flyer and capable of rapid dispersion. Not reported in the paper by Schoof and Siverly (45, pp. 830-838) was the fact that one adult of this species flew six miles from point of release in less than 24 hours. Of approximately 3463 tagged specimens releasted on October 30, 1952, 46 were subsequently recovered from 26 of the 69 trap stations. The recapture pattern for Phormia followed the same design as described for Musca. In a dispersal study of this species at Charleston, West Virginia, Schoof and Mail (43, p.462) reported rapid dispersal up to distances of six to 10 miles. Migration was not hampered by presence of wooded areas 400 to 500 feet in elevation, nor by watercourses. These workers conclude that P. regina could serve as a potential vector of pathogenic organisms over an area of eight to 20 miles in extent.

It appears well established that Phormia possesses extraordinary sense perception in locating food or potential breeding media. On June 19, 1955, the writer trapped several hundred specimens in his residential back yard in Corvallis, Oregon. The trap was baited with fish scraps for 24 hours. Normally, there are no flies of this species in that neighborhood, nor in any of the adjacent city blocks. Such incidents, however, are commonplace. Tales are legion of hunters who report the attraction of black blowflies to freshly killed carcasses in isolated areas.

In the Phoenix area, adults virtually disappear during July and August and are rarely observed or trapped (Figure 3). These

observations are consistent with the records of Deonier (12, p.67) who reports few, if any, P. regina trapped in the vicinity of Phoenix during the summer and early fall months of 1937 and 1938. Bishopp (2, p.327) mentions this species as quite troublesome around such commercial establishments as abattoirs and packing houses in Texas, but considers it essentially a cool-weather fly. According to James (31, p.76) cool weather favors development; in the south, Phormia becomes scarce during summers, and adults may be found out of doors during the entire winter as far north as Iowa. Haines, in southern Georgia (22, p.938) reared 235 adults from infested media collected in the fall, 4427 from winter collections, 817 from spring collections, but no Phormia were reared from summer collections. These observations tend to establish the fact that warm temperatures do not favor the abundance of adults. Hence, it is rather surprising to find that successful rearings of this species were completed, under conditions of both constant and variable temperatures, at mean temperatures as high as 88°F. Mean temperatures of 88° are not attained in Arizona until the last week of June or thereabouts. By this time Phormia adults have disappeared (Figure 3).

A few preliminary trials were run, under controlled conditions, in an attempt to ascertain the relative heat tolerances of Phormia regina and Musca domestica. These observations on caged flies suggest that Phormia adults are not as intolerant to high temperatures as their seasonal distribution might indicate. When adults of both

species were maintained at constant temperatures of 92°F. Phormia appeared to withstand these conditions as well as Musca, as long as water and sugar were constantly available. At constant temperatures of 95°F. there appeared to be higher initial Musca mortality. After 48 hours the mortalities in the respective cages became equalized. At the end of 72 hours, appreciably more Phormia were down. With Musca, heat tolerance appeared to be more of an "all-or-none" proposition; flies were either up or down. With Phormia, it was difficult to make positive counts during the progress of the experiments. Affected adults appeared unable to coordinate their wing movements; there was much buzzing and "bumbling" on the floor of the cage. It is impracticable to draw conclusions from only a few trials, but these results tend to confirm observations that Musca are more tolerant of high temperatures than Phormia.

Heat tolerance is probably influenced by diet. This subject, with all of its ramifications, could constitute an independent investigation. Schoof and Mail (43, p.258) report that in their Charleston flight range tests, abnormally hot weather caused an excessive mortality in the 400,000 flies reared for the study. However,[8] sugar was not provided for the caged flies, since these

[8]Personal communication with Dr. Schoof. Subsequent field experience at Phoenix revealed that provisioning with sugar served to reduce mortality in holding cages, without reduction in uptake of P^{32} in the milk, honey and water mixture also provided.

workers believed that sufficient sugar was present in the milk, honey and water mixture upon which the flies were allowed to feed, and that providing additional sugar might tend to reduce the numbers of flies feeding on the solution with attendant reduction in P^{32} uptake. Rasso and Fraenkel (42, p.644) report that sugar, as well as a suitable protein, is necessary for normal ovarian development in Phormia regina. The writer has observed large numbers of this species feeding on the flowers of spirea in bloom. Obviously, nectar from plants constitutes one source of sugar available in nature.

Humidity is another environmental factor which influences heat tolerance. Beattie (1, p.403) found that the thermal death point for Calliphora erythrocephala was definitely influenced by the factor of humdity. Saturated and dry air had the effect of lowering the thermal death point. Relative humidities from 60-80 percent were more favorable, with 70 percent relative humdity the optimum point.

The situation regarding temperature and activity relationships for Phormia regina is somewhat paradoxical. Obviously, the absence of this species during warm seasons cannot be explained by failure of development, or heat intolerance of the adults at mean temperatures of 90-92°F. (Table 20). It is doubtful if these high temperatures stimulate aestivation. Certainly the reactions of caged adults at high temperatures do not indicate this type of response.

The minimum period for 100% mortality of a given colony under

variable temperature conditions was 35 days. The maximum period for 100% mortality of any colony was 72 days, and the mean period was 52.0 days. Maximum longevity for caged adults, maintained at 80°F., extends from four to six weeks. Cool temperatures tend to increase longevity. Hall (23, p.168) reports that adults hibernate when temperatures drop too low for adult activity, and that hibernating adults may be found in tunnels of various wood-boring insects. In the vicinity of Charleston, West Virginia, P. regina probably passes the winter as a semi-active adult (37, p.676).

According to Miller, Doan and Wilson, (39, p.5):

> "P. regina has an oviposition range of from 20°C. to about 34°C. with an optimum near 26°C. At the lower temperatures, the longevity of the flies is greatly increased, but the number of eggs is greatly decreased. At the higher temperatures the number of eggs per female per day is increased but the total number of egg-laying days is decreased because the flies do not live as long. These two factors tend to equalize each other at the extremes but a temperature near 26°C. gives the greatest total deposition of eggs per female."

These workers give no figures for actual numbers of eggs produced.

In fecundity trials with caged females held at a rearing room temperature of approximately 80°F. over a period of 16 weeks, an average estimated yield of 355 eggs per fly was obtained.

Eucalliphora lilaea: Developmental rates at variable temperatures

Eucalliphora lilaea was reared in Phoenix under simulated field conditions during 1951 and 1952. Numbers of Eucalliphora

reared are shown in Table 35. The field rearing data for this species are given in Table 36. It may be noted, from Table 36, that members of three colonies which completed larval development failed to emerge as adults. In the case of one of these colonies which completed larval development during the winter of 1952, the cause for failure to emerge was undetermined, although insecticidal contamination was suspected. In the case of two colonies which completed larval development in May and June of 1952, their failure to emerge was due to heat injury. Pupae were held for several weeks. Upon examination these pupae were found to be non-viable.

For the most part, however, Eucalliphora lilaea is fairly easy to maintain under simulated field conditions, as long as mean temperatures do not exceed 85°F. Whereas Musca and Phormia are easier to maintain under constant temperatures than under variable temperatures, Eucalliphora appears better adapted to rearing, generally, under conditions where daily temperature fluctuations occur.

Temperature intervals used in deriving midpoint values for the field rearings are the same as those used with Musca and Phormia. The breakdown for developmental periods at various mean temperatures is given in Table 37. It may be noted from Table 37 that a number of colonies completed development at mean temperatures of 67°F. Eucalliphora lilaea is a cool weather species. Its developmental rates are very indicative of its seasonal prevalence. Field data for deriving developmental rates of egg to adult period, and the

increments of this period, are given in Tables 38 to 40. Deviations from linearity were insignificant in each case.

Eucalliphora lilaea: Developmental rates at constant temperatures

Rearing trials were run at five temperature settings (84°, 80°, 75°, 70°, and 65°F.) Each trial was replicated four times for both Corvallis and Phoenix strains (Tables 41 and 44).

No developmental periods are given for constant temperatures of 88°F. Since two colonies completed larval development under variable temperature conditions at mean values of 88°, some rearing trials were also attempted at this constant temperature setting but without appreciable success. Three colonies of the Corvallis strain were initiated. Two of these colonies finally completed development after 16 days but were undersized. The larvae of one colony perished in the media on the eighth day after seeding of eggs. Four colonies of the Phoenix strain were initiated. Three of these colonies appeared to pupate normally, but pupae checked on the 16th day after egg seeding were found to be non-viable. Larvae in one of the Phoenix colonies pupated when undersized. On the 21st day after seeding of eggs, these pupae were examined and also found to be non-viable. There appeared to be no difference in heat tolerance at 88°F. between the two strains of flies.

For the most part, the colonies reared at a constant temperature of 84°F. completed development, but the following symptoms

TABLE 35

Eucalliphora lilaea - Field Rearings

Mean Temperature		Numbers of Pupae	Numbers of Adults Reared		
			Male	Female	Total
61		282	123	115	238
64		406	168	219	387
67		1741	755	668	1423
73		134	59	63	122
76		266	117	127	244
79		631	204	331	535
82		280	123	137	260
85		430	172	204	376
	Total	4170	1721	1864	3585

TABLE 36

Field Rearing Data for Eucalliphora lilaea

Colony	Gen.	Larval Period	Temperature (°F.) Ave. Max.	Ave. Min.	Mean	Days	Pupal Period	Temperature (°F.) Ave. Max.	Ave. Min.	Mean	Days	Sum of Days	Mean Temp. Egg to Adult
E12	F-1	11/14/51-11/22/51	77.11	60.78	68.94	8	11/22/51-12/6/51	76.00	54.33	65.17	14	22	66.95
E13	F-1	11/19/51-12/2/51	77.64	56.29	66.96	13	12/2/51-12/17/51	72.38	49.88	61.13	15	28	63.76
E16	F-1	11/30/51-12/15/51	73.06	51.13	62.09	15	12/15/51-1/1/52	72.11	48.78	60.44	17	32	61.24
	F-2	1/24/52-2/8/52	83.13	53.19	68.16	15	2/8/52-2/20/52	75.62	52.30	63.96	12	27	66.16
	F-3	2/28/52-3/9/52	76.91	55.55	66.23	10	3/9/52-3/24/52	72.44	55.19	63.81	15	25	65.02
	F-4	4/1/52-4/8/52	92.25	67.38	79.81	7	4/8/52-4/17/52	86.60	66.50	77.56	9	16	78.03
E24	F-1	1/9/52-1/24/52	69.65	47.47	59.56	15	1/24/52-2/6/52	77.53	49.27	63.40	13	28	64.38
	F-2	2/20/52-3/4/52	79.43	54.79	67.11	13	3/4/52-3/19/52	74.75	55.88	65.31	15	28	66.10
	F-3	3/29/52-4/8/52	90.45	67.09	78.77	10	4/8/52-4/16/52	86.00	66.44	76.22	8	18	77.63
	F-4	4/25/52-5/2/52	85.25	68.13	76.69	7	5/2/52-5/12/52	95.64	73.55	84.59	10	17	81.06
	F-5	6/12/52-6/19/52	100.25	79.25	89.25	7	6/19/52-6/25/52	91.86	73.86	82.86	6	13	85.68
E27	F-1	1/17/52-1/27/52	74.36	51.09	62.73	10	1/27/52-2/8/52	84.38	54.13	69.27	12	22	66.33
	F-2	2/19/52-3/2/52	79.46	54.38	66.92	12	3/2/52-3/16/52	73.47	55.00	64.23	14	26	65.78
	F-3	3/26/52-4/3/52	88.78	64.11	76.44	8	4/3/52-4/12/52	88.80	67.20	78.00	9	17	77.22
	F-4	4/18/52-4/27/52	85.40	69.10	77.25	9	4/27/52-5/5/52	87.89	69.11	78.50	8	17	78.28
	F-5	5/10/52-5/18-52	96.00	72.22	84.11	8	5/18/52-5/25/52	97.50	74.63	86.06	7	15	85.25
E28	F-1	2/18/52-2/28/52	79.73	53.36	66.55	10	2/28/52-3/13/52	74.93	55.73	65.33	14	24	65.80
	F-2	3/24/52-4/2/52	87.50	62.70	75.10	9	4/2/52-4/11/52	89.50	67.50	78.50	9	18	76.76
	F-3	5/2/52-5/9/52	94.00	73.75	83.88	7	5/9/52-5/15/52	98.14	74.00	86.07	6	13	85.18
E15	F-1	11/30/51-12/13/51	72.57	51.93	62.25	13	12/13/51-12/31/51	72.37	49.21	60.79	18	31	61.38
E 7	F-1	11/9/51-11/20/51	77.70	61.1	69.40	11	11/20/51-12/3/51	77.14	56.14	66.64	13	24	67.59
E 4	F-1	11/7/51-11/18/51	76.50	61.50	69.00	11	11/18/51-12/3/51	77.50	56.38	66.94	15	26	67.79
E16	F-5	4/25/52-5/4/52	87.70	69.20	78.45	9	1 adult emerged - remainder died						
E26	F-1	1/14/52-1/27/52	75.50	58.29	66.89	13	1/27/52-2/10/52	only a few emerged			14		
E27	F-1	6/8/52-6/15-52	101.00	77.63	89.31	7	No emergence						

TABLE 37

Distribution of Developmental-Time Periods (days) for Eucalliphora lilaea field Rearings at Various Mean Temperatures

Temperature Interval	Midpoint of Interval	Developmental Periods In Days		
		Egg to Adult	Pupal	Egg plus larval
59.50-62.49	61	32,31	15,17,18	15,15,13
62.50-65.49	64	28,25,28	14,12,15,13 15,14,14	10
65.50-68,49	67	22,27,28,22,26,24,24,26	13,15	13,15,10,13,12 10,13
68.50-71.49	70		12	8,11,11
71.50-74.49	73	18		
74.50-77.49	76	17,18	8	7,8,9,9
77.50-80.49	79	16,17	9,9,8,9	7,10,9
80.50-83.49	82	17	6	
83.50-86.49	85	13,15,13	10,7,6	8,7
86.50-89.49	88			7,7

TABLE 41

Eucalliphora lilaea - Corvallis strain - Lab Rearings

Colony	Developmental Periods In Days: Egg plus larval	Pupal	Egg to Adult	Temperature
EC-6	10	11	21	65
EC-8	8	13	21	65
EC-12	8	12	20	65
EC-13	11	11	22	65
EC-23	7	11	18	70
EC-26	8	10	18	70
EC-32	8	12	20	70
EC-33	10	9	19	70
EC-2	7	9	16	75
EC-3	6	11	17	75
EC-9	5	8	13	75
EC-10	5	10	15	75
EC-24	6	8	14	80
EC-27	5	9	14	80
EC-29	6	9	15	80
EC-31	6	7	13	80
EC-4	5	11	16	84
EC-5	6	10	16	84
EC-18	7	7	14	84
EC-20	9	5	14	84

TABLE 44

Eucalliphora lilaea - Phoenix strain - Laboratory Rearings

Colony	Developmental Periods In Days: Egg plus larval	Pupal	Egg to Adult	Temperature
EP-2	10	12	22	65
EP-20	7	13	20	65
EP-28	9	14	23	65
EP-29	10	13	23	65
EP-6	6	12	18	70
EP-9	8	11	19	70
EP-15	9	11	20	70
EP-19	11	9	20	70
EP-3	7	8	15	75
EP-25	6	10	16	75
EP-26	6	9	15	75
EP-27	6	11	17	75
EP-7	5	9	14	80
EP-10	5	9	14	80
EP-12	5	8	13	80
EP-24	6	8	14	80
EP-1	7	7	14	84
EP-21	7	9	16	84
EP-22	5	9	14	84
EP-23	9	6	15	84

of heat injury were observed: (1) delayed emergence, extending over as long a period as four days, (2) variation in sizes of larvae of the same age, (3) over-activity of larvae, often resulting in migration from the media and subsequent starvation, (4) premature pupation and undersized pupae, (5) actual death of larvae, the larvae appearing flaccid, as if dropped in hot water, and (6) reduced vigor and shorter longevity of emerged adults.

Analyses of laboratory rearing data for developmental rates presented certain difficulties. Steps in these analyses are described in some detail. From inspection of the data given in Table 42, it may be noted that rearings indicate some retardation in developmental rate at 84°F. This retardation at 84° is evidently the cause for departure from linearity. When the rearings at this temperature are deleted, the hypothesis may be accepted that the regression of y on x is linear (Table 43). However, deleting the 84° rearings leaves a limited number of observations for a given strain.

During the rearing experience, no significant differences in temperature-developmental time relationships were observed between the two strains of Eucalliphora. These observations are confirmed by the test of hypothesis that the adjusted means of the two populations are equal. The end-point of calculations in the test of this hypothesis is as follows:

	d.f.	SS of x	SP	SS of y	Residual SS	Residual d.f.
Column	1	0.0	0.0	13.7813	13.7813	1
Error	30	1000.0	1767.50	3583.6875	459.6312	29
Total	31	1000.0	1767.50	3597.4688	473.4125	30

$$\frac{13.7813/1}{459.6312/29} = 0.87$$

One would accept this hypothesis, since at the 5% level of significance, F is less than 4.18 at 1 and 29 degrees of freedom. Essentially, then, the strains constitute one population as far as temperature-developmental time characteristics are concerned. Combining the rearing data for the two strains, and testing for linearity of egg to adult, the egg-plus-larval and pupal periods yields results which indicate that deviations from linearity are insignificant. However, of these three periods, only the pupal period indicates a linear relationship as high as 84°F. The linear relationship between temperature and developmental time of egg to adult, and egg-plus-larval stages only extends through 80° (Tables 45-48).

Eucalliphora lilaea: Comparison of developmental rates at variable and constant temperatures

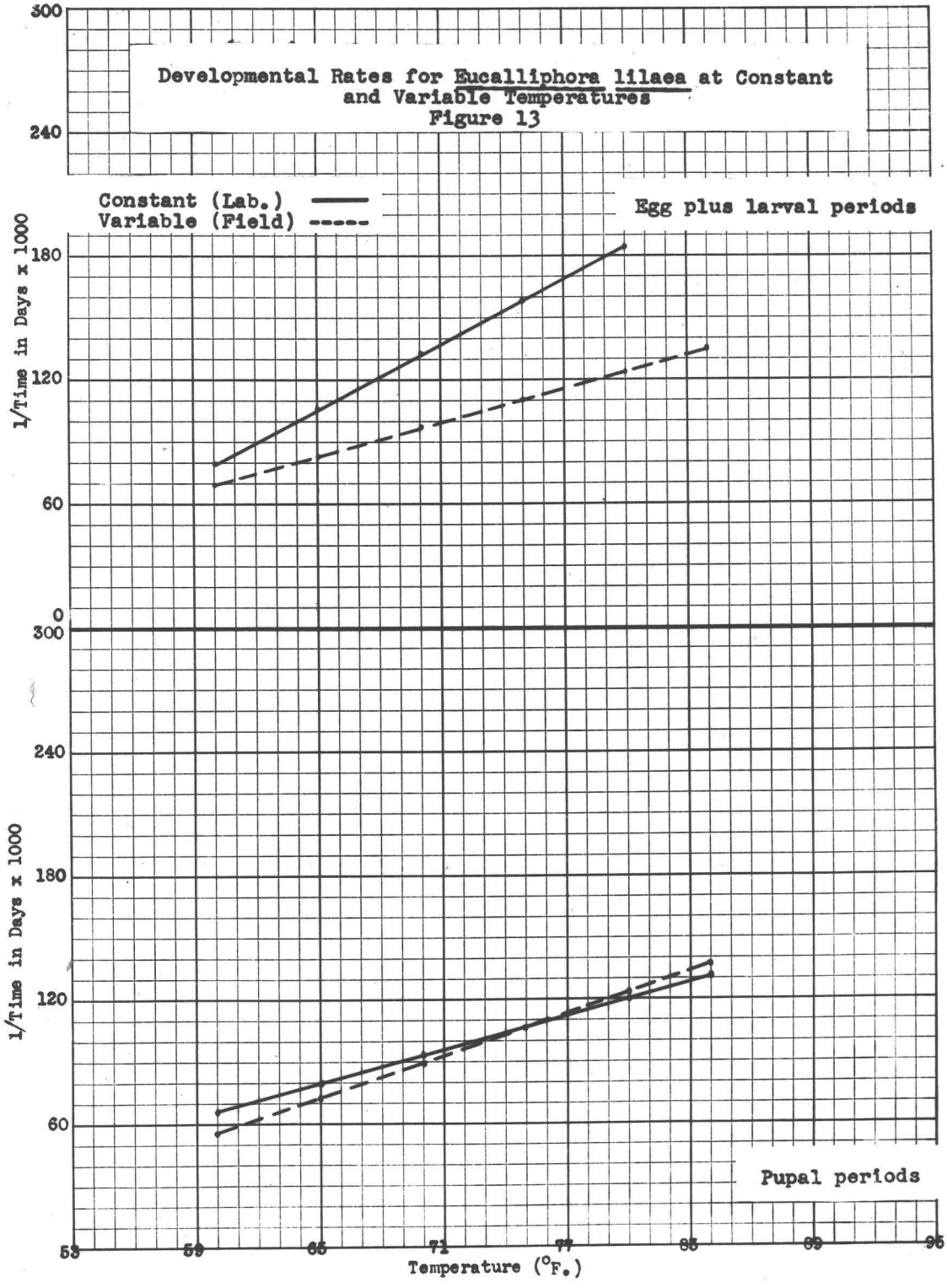
The hypothesis tested in Table 49a is accepted (F is less than 4.03). The hypothesis tested in 49b is rejected (F is more than 4.03). Hence, one would conclude that, as in the case of Musca and Phormia, the regression lines (shown in Figure 14) are

parallel but not identical. These regression lines indicate that development proceeds at a faster rate under constant than under variable temperatures. Also, as in the case of Musca and Phormia, egg and larval periods show relative retardation; the pupal periods, relative acceleration. Unlike Musca and Phormia, there appears to be better conformation to linearity with variable than with constant temperatures. Developmental-time periods for variable temperature rearings also show linear relationship to wider ranges of temperatures than do the periods for the constant temperature rearings. Figures 13, 14 and 15 show developmental rates derived for egg to adult egg-plus-larval, and pupal periods of Eucalliphora lilaea at both variable and constant temperatures. Calculations for these graphs are given in Table 50.

The temperature-developmental time relationships of this species constitute a major factor in determining its seasonal prevalence (Figure 3). In contrast to Phormia, other biological factors play a relatively minor role in this respect. However, mention may be made of such factors as breeding habits, distribution, longevity and fecundity.

Eucalliphora lilaea: other biological factors

In its utilization of various kinds of production media, Eucalliphora may occupy an intermediate position between Musca and Phormia. Larvae of this species were recovered from eight of 21 different classifications of media. Of 50 samples positive


Developmental Rates for Eucalliphora lilaea at Constant and Variable Temperatures
Figure 13
Constant (Lab.)
Variable (Field)
Egg plus larval periods
Pupal periods
1/Time in Days x 1000
300
240
180
120
60
0
53
59
65
71
77
83
89
95
Temperature (°F.)

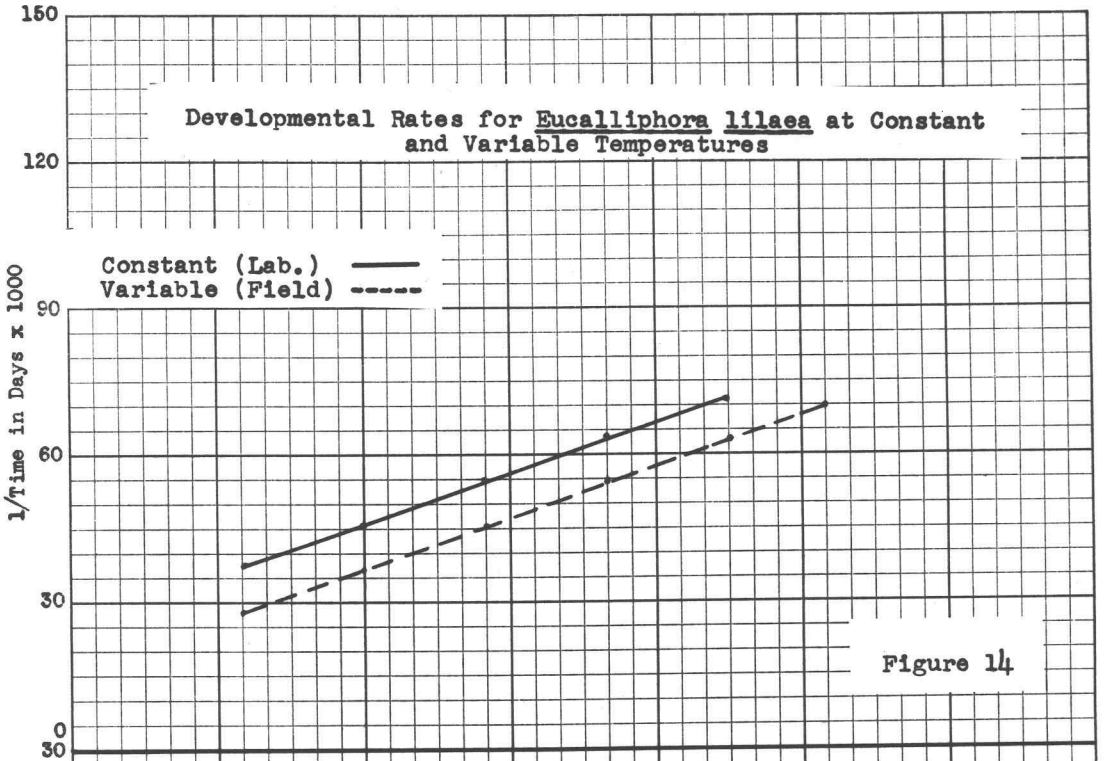


Figure 14

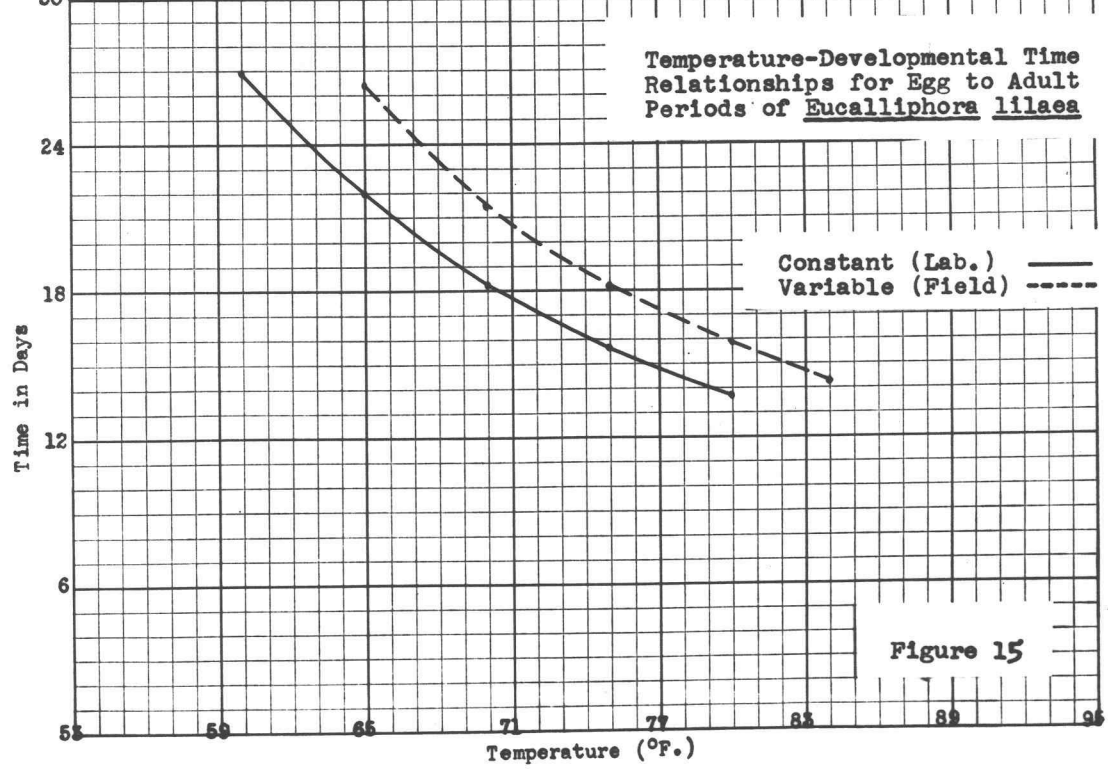


Figure 15

for larvae, 31 of these were samples of contained garbage. Other substrates utilized were chicken excrement, scattered garbage, commercial wastes, coffee grounds, dead animals, seafood wastes, and waste vegetables. In Phoenix, no samples positive for this species were recovered during summer and fall months (51).

There is good indication that Eucalliphora is able to utilize excrements and composted material as production media. Like Musca, it is able to utilize soil which has become impregnated with waste organic matter. The writer once observed hundreds of newly emerged Eucalliphora on the lawn of a well-maintained residence in Phoenix. One small area, about six feet in diameter, appeared to be the focal point of activity. In response to questioning, the residents reported that waste water from cleaning fish had been dumped in this small area over the past several months. Pupae were numerous in the upper layer of the soil. The writer has identified Calliphora terrae-novae larvae collected from garden soil in Oregon. Eucalliphora and Calliphora are closely related genera. Eucalliphora can be reared in the same synthetic medium as that used for rearing Phormia regina.

According to Hall (23, p.286) Eucalliphora lilaea is Nearctic in its distribution; in the United States occurring most frequently in Rocky Mountain states north of Colorado. Data from the five-city program indicate that Eucalliphora lilaea were recovered from trap samples in the vicinity of Topeka, Kansas in May and June, and in the vicinity of Charleston, West Virginia, in May, June,

September and October. These trap data show only that Eucalliphora was present during those particular months and give no indication of its relative abundance. The assumption is that they were scarce. This species was never taken at the Michigan and New York projects.[9]

Longevity data were obtained from sustained adults reared under simulated field conditions. The minimum period for 100% mortality of a given colony was 21 days. The maximum period for 100% mortality of any colony was 47 days, and the mean period was 43.5 days. With successively-reared generations, time intervals in days between emergences of adults were: minimum, 17; maximum, 47; mean, 29.3. Based on occurrence during a maximum of eight months of the year, there may be as many as eight annual generations in the Phoenix area. Observations on caged adults indicate that females are capable of producing as many as 400 eggs during their lifetimes.

Comparison of developmental rates for Musca, Phormia and Eucalliphora

Some additional Musca rearings were conducted that are not included in Tables 8 and 12. Results, in terms of days to complete egg-to-adult development for six replicated rearings of each strain of Musca at constant temperatures of 92 and 95 degrees F. are as follows:

[9] Schoof, H. F. United States Public Health Service, Communicable Disease Center, Technical Development Laboratories, Savannah, Georgia. Personal correspondence dated July 13, 1955.

Corvallis strain		Phoenix strain	
92°	95°	92°	95°
8	9	7	9
8	7	9	9
7	7	8	7
9	7	8	7
8	7	7	7
8	7	8	7

When these two additional arrays are appended to each of the six arrays given in Tables 8 and 12, the b and r values derived are but slightly different than when only six arrays of y are used. In other words, these results indicate that development proceeds at the same rate for Musca from 65 to 95, as from 65 to 88 degrees F. There is no significant retardation in development at these higher temperatures. Regression and correlation coefficients for this extended range of temperatures are the values given for Musca in Table 51. Parenthetical values, in each case, are the correlation coefficients.

The tests of hypothesis indicated that for each species regression lines were parallel, but not identical. Although regression coefficients are consistently higher for constant temperature rearings than for variable temperature rearings (Table 51), there is insufficient reason to believe that these differences are significant. Rearings at constant and at variable temperatures are actually more comparable than is immediately apparent.

The fact that each overall developmental period consists of two definite components - egg-plus-larval and pupal period -

allows the possibility for further analyses. It may be noted from Table 51 that developmental rates for egg-plus-larval periods are consistently slower at variable temperatures than at constant temperatures, but that pupal development is consistently faster at variable temperatures. However, it should also be noted that pupal periods for each species were "handicapped" by an initial lag due to retardation during egg and larval periods. Figure 13 illustrates this relationship quite clearly for Eucalliphora lilaea. The close relationship between developmental rates for pupal periods as depicted in Figure 13 suggests the possibility that the adjusted means for these two populations are equal. Results obtained from testing hypotheses (Tables 52a, 52b) indicate acceptance for Musca (F is less than 3.09) as well as for the Eucalliphora rearings (F is less than 4.00). The F value is in the rejection region for Phormia (Table 52c), since this value at the 5% level of significance exceeds 3.11 at 2 and 79 degrees of freedom. However, this value of 8.88 is a great deal closer to the acceptance region than the value of 260.51 obtained in Table 32b for overall developmental periods. For Phormia, developmental rate at variable temperatures is more closely comparable to the rate of egg-plus-larval period of development under constant temperatures (Table 52d).

These additional analyses serve to determine more specifically the reasons for slower overall developmental rate at variable temperatures: daily subjection to inconstant temperatures appears to retard larval development. This is especially applicable to

Phormia.

It is quite desirable that one set of regression coefficients be derived as a basis for constructing graphs that will show comparitive temperature-developmental time relationships of the three species. Probably the best basis for deriving these regression coefficients is by a weighted average of b values for laboratory and simulated field rearings. Actually, there is justification in doing so, even though the constant temperature rearings show consistently higher rates. In nature, larvae are quite capable of independent locomotion, and will migrate into those portions of the media where temperatures are most optimum for development. Generally, much bulkier media are infested than those used in artificial rearing. Blowflies infesting animal carcasses will often burrow into the middle of a carcass, and concentrations of larvae will be found at the ground layer under the carcass. Housefly larvae are capable of penetrating several feet into animal excrement or other bulky media. Thus, the micro-environments which these larvae occupy are probably less subject to variations in temperature than if they were exposed, yet temperatures are seldom as constant as under controlled conditions.

The mean regression coefficients shown in Table 51 are obtained by a weighted mean of b values for laboratory and simulated field rearings. The $\bar{y}$ and $\bar{x}$ values (e.g. 88.1774 and 80.6600) are also based on weighted mean values from these two sets of data. Regression curves constructed from the formulas for $\bar{y}x$

are shown in Figure 16. Temperature-developmental time relationships for the same data are shown in Figure 17. The dotted extremities of the lines in both graphs represent extrapolations. Distances of extrapolation do not exceed five degrees Fahrenheit.

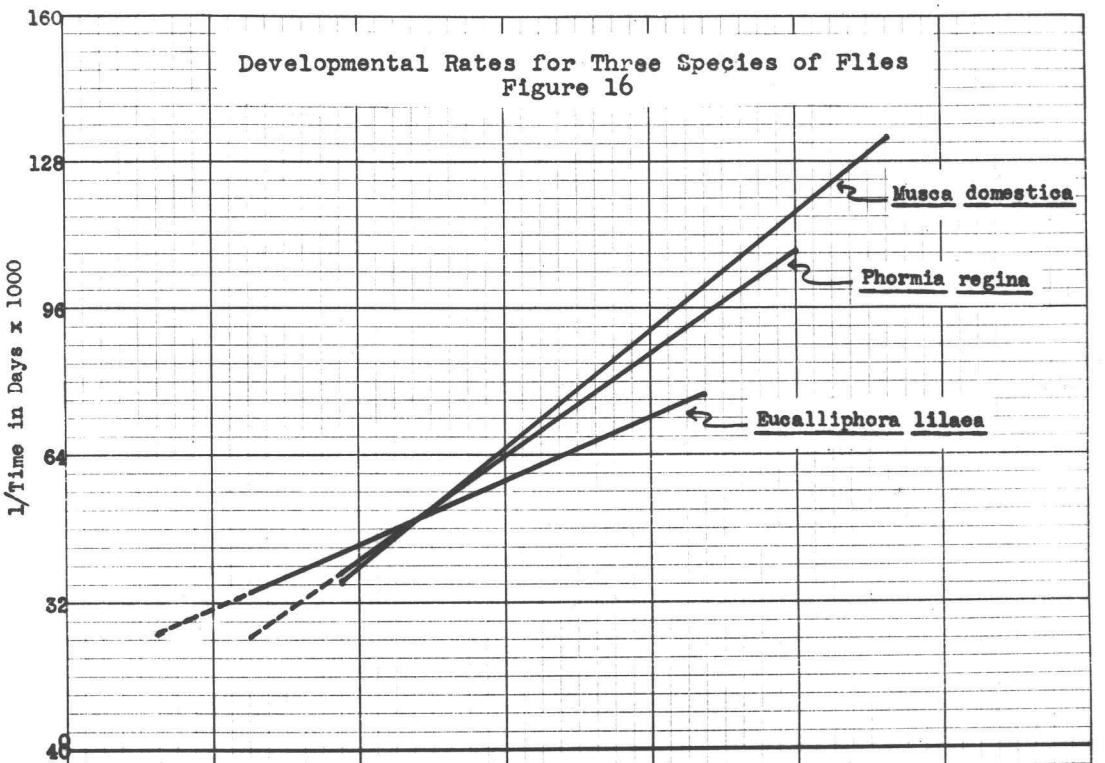
Some retardation in development was noted for Eucalliphora at constant temperatures of 84°F. However, as indicated by the simulated field rearings, at a somewhat slower rate of development this retardation would not be significant, and development would probably extend in linear relationship as high as 85° under field conditions.

Rearings notes on other species studied

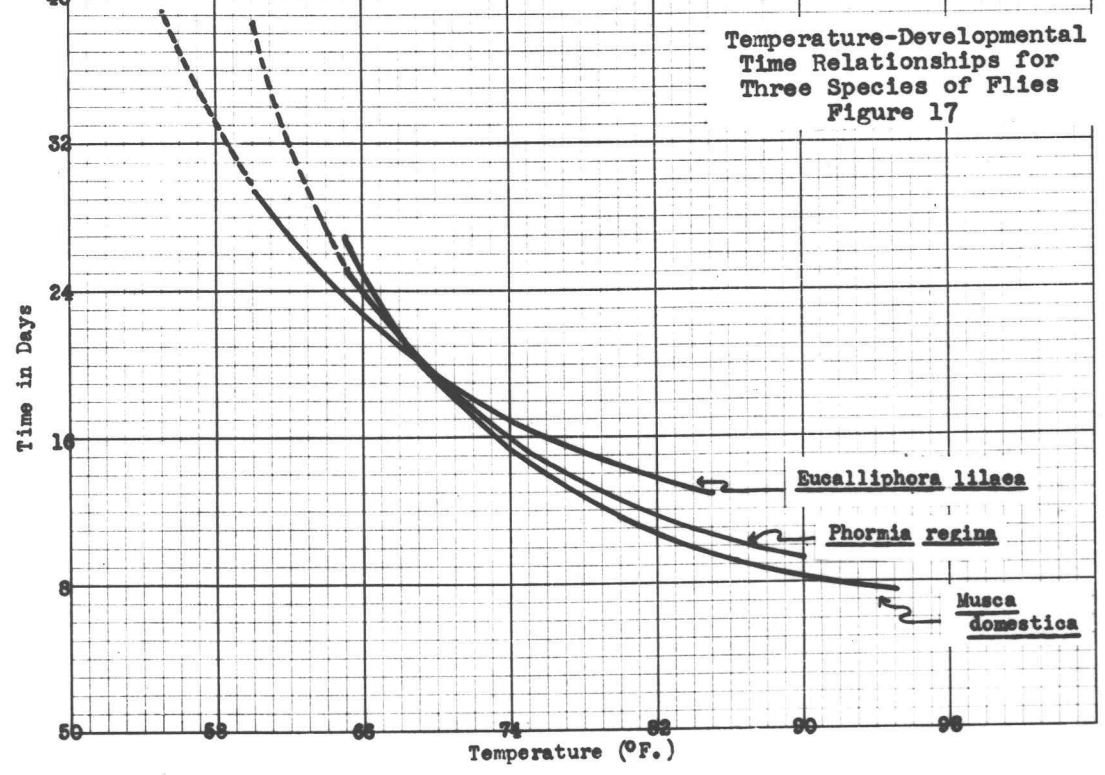
There appears to be little, if any, reported information on the biologies of two other species of flies which were reared in this study: Aldrichina grahami (Aldrich) and Sarcophaga plinthopyga Wiedemann. The findings pertaining to these two species will be briefly reviewed.

Aldrichina grahami is similar in appearance and habits to Eucalliphora lilaea. According to Hall (23, p.291) none of the habits or details of the biology of this species are known. A. grahami is not abundant in the Phoenix area, but from previous trap surveys it was evident that this species of blowfly was limited in its occurrence and seasonal prevalence, specimens having been obtained in only a few specific city blocks during previous winter seasons. After repeated attempts, one gravid female was finally

Developmental Rates for Three Species of Flies
Figure 16



Temperature-Developmental Time Relationships for Three Species of Flies
Figure 17



trapped in one of the same sub-standard residential blocks where A. grahami had been previously collected.

This species appeared to be well adapted to the rearing methods employed. Five successive generations were reared between January and June of 1952. Time ranges in the various phases of the developmental cycle are as follows: egg-plus-larval period, 7-17 days; pupal period, 7-15 days, and pre-oviposition period, 4 to 21 days. Although mean temperatures of 80°F. under simulated field conditions appear optimum for its development, immature stages may complete their development at much lower temperatures, and emergence of adults was observed at 46°F. This species appears quite susceptible to heat injury. At mean temperatures of 86°, where maximum readings exceed 100°, there appears to be some retardation in development. At mean temperatures of 90° and maximum readings more than 100°, larvae perish and adults live but a few days. Dormant pupae held over from late spring until fall were not viable.

It was determined that one female may oviposit more than 200 eggs in a batch. From a single mating, approximately 8840 progeny were reared in less than two months. Of this number 4243 were males and 4597 were females. Although this species is apparently unable to adapt to warm weather conditions, as many as six annual generations may be produced in the Phoenix area. In California, where Hall (23, p.191) reports that adults have been collected during almost the entire year, it is conceivable that 12 annual generations may be produced.

Hall (23, p.190) states that Aldrichina grahami is indigenous to Asia, and has evidently been imported into the western part of the United States in comparatively recent years. In the United States it is typically an extreme western form. This species was never recovered at projects other than Phoenix in the five-city program. The writer has collected this species in Corvallis, Oregon from traps baited with decaying meat.

Sarcophaga plinthopyga, one of the flesh flies, was the only representative of the Sarcophagidae studied. Since this species is larviparous, overall developmental time is considered as the interim between deposition of the larvae and adult emergence. Duration of larval, pupal and pre-larviposition periods are as follows: larva, 7-52 days, pupa, 6-32 days, pre-larviposition period, 11-35 days. Intervals between generations were: minimum, 26 days; maximum, 80 days; mean, 38.7 days.

Members of the Sarcophagidae appear to pass the winter in central Arizona as semi-active adults. They have often been observed resting in sunny locations during cool months of the year. Low temperatures retard the developmental cycle. A developmental period of 83 days for S. plinthopyga was the longest observed in this study.

According to Harold R. Dodge,[10] S. plinthopyga has two

[10] Personal correspondence, March 27, 1953

markedly different types of first instar larvae, but only one of these types occurs in the Phoenix area. The first instar period must be of short duration; the larvae were observed to make tremendous growth during the first two days after deposition. This initial growth rate may be an adaptation for the species in utilizing breeding media which is subject to rapid dessication[11], or in competing with other saprophytic forms of animal life present in the media. According to James (31, p.51) the larvae differ in their breeding habits and are commonly found on carcasses or as parasites in the bodies of insects. They have been known to produce myiasis in man.

James (31, p.43) states that gravid females of the genus Sarcophaga produce, on an average, from 20 to 40 larvae, although some species produce more progeny than others. The low reproductive capacity and relatively slow developmental period would appear to be factors which limit abundance of Sarcophaga plinthopyga in temperate regions.

[11]Cow droppings in pastures and dog stools on lawns are often infested with Sarcophagid larvae. In dry climates, such exposed media often dessicate in a matter of hours, yet the larvae are able to complete development.

DISCUSSION

Development at constant and at variable temperatures

The literature is quite extensive on the topic of constant versus variable temperatures and their effects on insect development. A number of papers have been written reporting results applicable to representatives of several orders of insects. Reviewers have studied these papers and sought to generalize, for the sake of formulating a principle which would be broadly applicable to insects as a group. A fairly recent review by Cloudsley-Thompson (9, pp.183-189) treats of this topic and includes a rather comprehensive bibliography. One of the best known reviews is that of Uvarov (54, pp.1-279). In summarizing the evidence relating to temperature effects, Uvarov states:

> "It is too early to draw any definite conclusions from the evidence .... One point, however, is beyond dispute, namely, that fluctuations of temperature are not without an effect on the rate of development. This effect is often positive, particularly when a favorable temperature alternates with one below the zero of development (but not low enough to be injurious) while an alternation with high temperature is usually harmful."

Some of Uvarov's conclusions appear to be based upon the work of Ludwig and Cable (35, pp.493-508) who state, in their conclusions, that

> "If one of the temperatures is above the optimum for development and the other is between theoretical threshold and the optimum, development appears to be retarded .... If one temperature is between the theoretical

> threshold and the actual threshold of development, the rate is accelerated. This acceleration is due to development which occurs at temperatures below the theoretical threshold."

Uvarov also reviews the work of Peairs (41, p.53) who states, as his sixth conclusion:

> "Development has been found to be accelerated by variations in the daily temperature when compared with constant temperature of the same apparent value."

The question of whether variable temperatures serve to retard or accelerate development is actually a side-issue, and not an objective of this study. Inasmuch as certain of the results in this study are not in complete agreement with such generalizations as those stated above, the topic merits some discussion in this paper.

Peairs' work is one of the pioneer investigations in this area, and due credit should be allowed for his part in the development of the principle of linear relationship which exists between temperature and developmental rates. However, there are certain points - especially in his analysis of the data - which warrant examination.

Peairs (41, p.53) based his "velocity of development" curves upon the "best fitting straight line .... determined by the method of least squares." There is nothing to indicate if this "best fitting straight line" so derived is an efficient unbiased estimate. He conducted his rearings for Musca domestica, Lucilia caesar and Calliphora vomitoria at temperatures extending from 35 to 8 degrees Centigrade. It is difficult to see how a linear

relationship would apply to such an extended range. Had Pearis used the test for linearity, the results would probably have been significant, leading him to a different interpretation. Bucher, Cameron and Wilkes (6, p.56) present good evidence that for housefly puparia, between 17 and 34°C. the rate of development is clearly a linear function of temperature, but that below 17°C. the rate varies not directly, but with the logarithm of the temperature.

Pearis states, with reference to a table showing developmental time for blowflies reared at both constant and variable temperatures, "the acceleration is slight in extent, at its greatest being little more than the variation encountered in different lots at constant temperatures." Yet he continues, "there is some acceleration which may be attributed to outdoor conditions as compared with incubator conditions." There are no data given on maximum or minimum temperatures, and the outdoor rearings which he reports were all conducted at temperatures with mean values in a restricted range between 20.5 and 21.2°C. The remainder of his rearings at variable temperatures were conducted by moving, manually, the colonies from one incubator to another incubator with a different temperature setting. In other words, the variable temperatures in Pearis' experiments are hardly comparable to the temperature variations encountered in the normal outdoor environment of the test insects.

The final point of examination regarding Pearis' paper is the fact that his conclusion regarding developmental-rate differences

is not supported by statistical inference. Peairs presents (41, p.45) an analysis, using Harris' method for determining goodness of fit, but this analysis simply shows significant differences between minimum and mean developmental periods of the same rearings. In seeking to account for acceleration at variable temperatures, Peairs states (46, p.38) that:

> "a speculative reason might be that the protoplasm of these organisms is adapted to variable conditions and that variable temperatures constitute a normal environment while constant temperatures are abnormal and so retard development."

Peairs does not attempt to explain if blowfly and housefly larvae, when involved as myiasis producers in man and other warm-blooded animals, occupy a normal or abnormal environment.

There is disagreement among other workers who utilized mosquitoes as test insects. Headlee, working with Aedes aegypti, published a series of three papers on the relative effects on insect metabolism of temperatures derived from constant and variable sources. Based on results of the first set of experiments (24, p.364) he concludes that under three sets of variable temperatures (50-80, 60-90, 70-100F.°) and with concurrent constant temperature experiments being run at the means of the variables (65, 75, and 85°F.) there appeared to be no significant difference in developmental period at 65°, but constant temperatures were associated with faster developmental periods at constants of 75° and 85°F. From further work done with Aedes aegypti (25, p.174) Headlee concludes that the relative effects of constant and variable temperatures on insect's development depends upon where in the range

of the insect's normal temperature these constant and variable temperatures lie; that the underlying and governing factor is the accumulation of the required amount of temperature, regardless of whether the temperature in question comes from constant or variable sources. In the third paper in the series, (26, p.786) Headlee states that with Aedes aegypti, the ratio between developmental time under constant and under variable temperatures shows no significant difference except in the lowest range, where 55 days were required to complete development at variable temperatures with a mean of 60°F. while only 38.5 days were required to complete development at the same mean temperature under constant temperature conditions.

Huffaker, (30, p.25) basing his conclusions on work done with Anopheles quadrimaculatus, disagrees pointedly with Headlee, maintaining that development at variable temperatures is faster, generally, than at constant temperatures. Huffaker maintains that Headlee misinterpreted his own data. Huffaker proposes that the reciprocal of the catenary curve seems to be the most adequate and adaptable method yet advanced for expressing the relation of temperature to the velocity of insect development. However, his conclusions are not based upon statistical inference. Huffaker does not report a test of his data to determine if deviations from his proposed curves were significant; his curves appear to be derived empirically. Neither Headlee nor Huffaker report testing results obtained under constant versus variable

temperatures to establish whether differences were significant or insignificant. In both cases, variable temperatures were artificially induced by moving colonies from one constant temperature to another.

Thus, it appears from a sampling of the literature as it pertains to Diptera that contradictions exist, and that more evidence, based upon efficient, unbiased inference should be considered before formulation of principles.

There are two factors which might account for the retardation in developmental rate of the three species of flies reared under field conditions. In order to obtain data on pre-oviposition periods, a number of these rearings consisted of successively-reared generations, using the first eggs produced. It is possible that progeny produced from initial ovipositions may be slower in development than progeny produced from later ovipositions. Secondly, mean temperatures were calculated by the U. S. Weather Bureau method of obtaining averaged values. If the mean temperature values derived by this method are slightly higher than actual, the reported rates of development are slower than actual. Nevertheless, making due allowance for these factors, the generalization that variable temperatures accelerate development is not applicable to the situation encountered under simulated field conditions on this problem. Neither is the generalization applicable that exposure to low temperatures accelerates development, while exposure to high temperatures retards development.

It seems reasonable that the extent and consistency of variations in temperature should be considered before generalizing upon temperature effects. There are sharp fluctuations in daily temperatures in desert areas; winter temperatures in Phoenix often cycle between maximum readings of 85°F. to minimums of 40°F. within one 24-hour period. Rearings which approximate these conditions reveal no significant retardations at high temperatures or accelerations at low temperatures. There is no retardation of Musca or Phormia when maximum temperatures attain 100°F. Eucalliphora appears to withstand mean temperatures of 84°, with maximums of 95°, with no apparent retardation in developmental rate. The general effect of exposures to variable temperatures appears to be that of retardation in overall rate of development. In the case of Eucalliphora, this retardation is associated with linear relationship over a wider temperature range than is evident from developmental rate under constant temperature conditions.

Bliss (4, p.495) found that exposing larvae of Drosophila melanogaster to low temperatures prior to puparium formation lengthened the pre-pupal stage. The retardation of larval development with the flies used in this study does not appear to be identifiable with high or low temperature ranges but rather throughout the entire temperature ranges of the simulated field rearings.

It is noteworthy that Ludwig and Cable (35, p.508) derived their conclusions concerning accelerating effects of variable temperatures working with pupae of Drosophila melanogaster, while

Bliss formed his conclusion regarding the retardation effects from working with larvae of the same species. Ludwig and Cable did not base their conclusions on statistical inference. In the case of Musca and Eucalliphora (Figures 9 and 13) the pupal periods appear to show a faster rate at variable than at constant temperatures. Actually, these differences are statistically insignificant (Tables 52a, 52b).

Variations in temperature could have different effects on different stages of development. "All the pupae have to do is metabolize" - while larvae, in order to develop, have to feed. Perhaps variable temperatures, particularly if the diurnal range of variation is wide and inconsistent in extremes, serve to modify feeding or locomotor reactions which in turn affect developmental rates.

In many of the accounts dealing with temperature-developmental time relationships, the terms "threshold temperature" and "constant" are used. Peairs defines these terms (41, pp.6,7). One of the best explanations for derivation of threshold temperature and constant values is in a paper by Larsen and Thomsen (33, pp.1-75), two Danish workers, who investigated temperature-developmental time relationships for five species of muscoid flies. Musca domestica was one of the species reared. All rearings in their study were conducted under constant temperature conditions. These workers ran several replicates at each temperature setting, but considered only the minimum developmental-time intervals in

deriving developmental rates. Larsen and Thomsen used horse excrement for rearing their flies, since they believed this to be the natural medium for fly development. However, they believed it to be an insoluble task to keep such a medium constant; they observed considerable variation among replicated rearings in this medium (33, p.14). Their method of treating this variation was to disregard it, by using only minimum time-intervals in their analyses of data.

The formula $t = \frac{\text{constant}}{T - c}$ (33, pp.16,17), where t is the duration of development, T the registered temperature and c the threshold of development, - may be used in deriving points for construction of a hyperbolic curve. Derivation of c, the constant, is obtained by selecting two time values, with corresponding temperature values. Preferably these sets of figures should be selected at opposite ends of a temperature range (e.g. 10 days at 90°F. and 30 days at 60°F.). Using this example,

$$10\ (90 - c) = 30\ (60 - c),$$

$$c = 45$$

Substituting the value of 45 in the equation above,

$$10 = \frac{\text{constant}}{90 - 45} \qquad \text{or} \qquad 30 = \frac{\text{constant}}{60 - 45}$$

yields a value for constant of 450. Plotting the values obtained for 90° and 60°, and all the intermediate points between these two temperature values will give a perfect hyperbolic curve.

Larsen and Thomsen (33, pp.16,17) selected these points

empirically. They plotted results against the hyperbola, and observed that at lower temperatures, 16°C. and below, the duration of development was generally shorter than the theoretically expected values. There is good reason for this dispersion. The reciprocals of these time values would, in the case of the example used, yield a straight line between 90 and 60°F. Extrapolation would extend the straight line to 45°F., or theoretically, to the threshold of development. It is exceedingly risky to extrapolate for a distance of 15 degrees, since the linear relationship between temperature and developmental-time is applicable to only a limited part of the temperature range. Yet, this method of deriving threshold and constant values is commonly employed. The dispersion from the hyperbola is an expression of departure from linearity in rate of development. As mentioned previously, there is evidence that this departure from linearity, in the case of housefly larvae, begins at 17°C. (6, p.56). Below 17°C. the rate appears to vary with the logarithm of the temperature.

Clearly, the method of deriving developmental rates by the linear regression method has distinct advantages over the "threshold and constant" method. Since there is no need to select empirical values for construction of curves, the linear regression method is unbiased. The test for linearity is a test of the efficiency of the method. The mean of the sample regression coefficients (b) is the population regression coefficient (beta). Thus, data derived by this method are unbiased efficient estimates of

populations and can be used in making comparisons with data from other samples. "Constant" and "threshold" values are not required. However, if for any reason these values are desired, they may be quite simply derived by merely substituting values for $\bar{y}x$ at any two temperature points and using these values in obtaining the "constant", instead of empirical values.

A considerable portion of Larsen's and Thomsen's results, including an account of their use of the formula for a catenary curve, is given in the book by West (56, pp.191-207). Their empirical curve shows a somewhat faster rate than the developmental rates derived for Musca domestica in this study. Comparison of days developmental time (as shown by hyperbolic curves) for the two studies is as follows:

	95°F.	86°F.	77°F.	68°F.
Larsen and Thomsen	7.5	8.0	11.7	17.5
Present study	7.5	9.5	13.4	21.0

A faster rate would be expected, since Larsen and Thomsen used only minimum time intervals. However, they report some retardation at 40°C. (95°F.). They also report that temperatures of 40°C. prevents normal pupation; that at 40°C. this injurious effect is so great that as a rule no flies emerge (33, p.23). Evidently, the houseflies that Larsen and Thomsen worked with were adapted to cooler temperatures than certain strains of houseflies indigenous to the United States. Phoenix flies appeared to undergo no retardation in development when temperatures attained 95°F. Flies of the Corvallis strain are reared in artificial medium in

the Entomology Rearing Room at Oregon State College. Temperatures in the battery jars often reach 41-43°C. without apparent injurious effect. According to Chemical Specialties Manufacturers Association standards (8, p.244), maximum temperatures in rearing jars should not exceed 130°F. (54.4°C.).

Considerable variation exists in temperature-developmental time results reported for Musca domestica by workers from various parts of the world. West (56, pp.199-204) reviews the literature on this topic. It would be difficult for individuals responsible for fly control efforts in any given community to reconcile this variance in reported results and arrive at data which would be applicable to a local problem. Workers would benefit by conducting their own rearings; results obtained thereby would be the most applicable in arriving at cultural control recommendations for the problem at hand.

Correlation of biological factors with seasonal prevalence

Two main lines of evidence are considered in obtaining a better understanding of seasonal prevalence: (1) temperature-developmental time relationships, or developmental rates and (2) other biological factors, such as longevity, fecundity, and temperature-activity relationships. Developmental rates play a major role in determining seasonal prevalence of Musca domestica and Eucalliphora lilaea. All biological factors require consideration in attempting to explain seasonal prevalence of Phormia regina.

Figures 1, 2, 3 and 16 or 17 serve as points of reference for this discussion. In Figures 1 and 3, it was noted that variation in the typical bimodal curve effect for adult fly densities in the Phoenix area was not accountable on the basis of differences in temperature. This curve for total fly populations, especially for the summer months, is very indicative of the seasonal trends for Musca domestica alone. If not temperature, what factor or factors serve to limit the abundance of Musca during the summer season?

An analysis of the conditions responsible for fly production suggests the best explanation in this case. Of the five factors[12] essential for fly production, the one most likely to be critical during summer months is moisture. Because of differences in crop yield, such media as canteloupe and watermelon are more abundant during certain seasons than others. In 1950, the melon crop was extensive in the Salt River Valley of Arizona. The extent to which this condition can effect adult fly densities is almost beyond belief. Waste canteloupe constitutes the best housefly-breeding medium observed in the writer's experience. This subject is treated more fully in the second of a series of three papers reporting utilization of fly production media (51).

[12]These five factors are considered to be: available food, moisture, warmth, oxygen and time. Absence of any of these five factors is limiting.

Although Musca domestica has a rapid developmental rate, its predominance in southern parts of the United States can hardly be attributed to this factor alone. Housefly adults are noted for their ability to disperse, to seek out and feed upon a wide variety of substances. However, the larvae of houseflies deserve as much notoriety for their wide utilization of breeding media as do the adults for their omnivorous tastes. The versatility of Musca in utilization of breeding media, plus adult as well as pre-imaginal adaptation to high temperatures are additive factors in accounting for predominance in such areas.

Successful adaptation of houseflies in many areas is coincident with high degree of insecticidal resistance. This development of insecticidal resistance has served to shift emphasis to forms of cultural control. However, basic research in all phases of life history is indicated as a basis for cultural control recommendations. Findings in this study imply that such recommendations are most applicable if investigations are conducted within the study area.

Developmental rates for Phormia may account, in large measure, for its initial peak populations occurring earlier in the year than those of Musca domestica (Figure 3). Below mean temperatures of about 70°F., developmental rates are faster for Phormia than for Musca (Figure 16).

Based on trap surveys, the occurrence of initial peak populations of Phormia precedent to Musca was observed not only in

Phoenix, but in three of the other cities participating in the five-city program (44, pp.5,8). At the Topeka, Kansas project, initial peaks of Phormia occurred in June; initial peaks of Musca occurred in July and August. Likewise, at the Charleston, West Virginia project, initial peaks of Phormia occurred in June; initial peaks of Musca occurred in July and August. At the Muskegon, Michigan project, initial peaks of Phormia occurred in July; initial peaks of Musca extended from July into August. At the Troy, New York project, initial peaks of both species did not occur until late August. However, at Troy, Phormia abundance far exceeded that of Musca. Evidently, from these data as reported by Schoof and Savage (44, pp.3,5,8), peak populations of Musca would not be expected until average monthly temperatures attain 70°F., while peak populations of Phormia may occur during periods when average monthly temperatures are less than 70°F.

Why are peak populations of Phormia not sustained through warm periods? The heat tolerance of both adults and larvae is much greater than might be expected. Consequently, the absence of this species during summers in southern United States cannot be attributed to heat injury in either pre-imaginal or adult stages. The adaptive factors of Musca, previously discussed, would force Phormia to second place under stress of competition. Certain species of Calliphoridae commonly associated with Phormia during other seasons of the year (Phaenicia sericata, Callitroga macellaria) are also present throughout summers.

Nicholson (40, p.98) reports a temperature preference range for Lucilia (= Phaenicia) sericata of from 20 to 35°C. (68 to 95°F.). However, P. sericata adults are observed during somewhat warmer periods of the year than Phormia. Deonier (11, p.169) observed adults of P. sericata active about carcasses at minimum temperatures of 51°F.; adults of Phormia were active at temperatures as low as 40°. Stewart and Roessler (53, p.110) report trapping Phormia in the southern part of the Sacramento Valley in California throughout the summers of 1935 and 1936. It is difficult to determine temperatures from the data given by these two authors, but it appears that maximum temperatures rarely exceeded 100°F. and mean temperatures 80° over the entire trapping period. Williams (57, p.557) reports Phormia regina as prevalent in New York City from June 16 to September 15, representing 14.2 percent of total trapped flies. No temperature data are given.

The total absence of Phormia in Phoenix during the warmest part of the year remains something of an enigma. This species was observed during summers at altitudes of 4000 feet, less than 100 miles from Phoenix. Since it is notably a strong flyer, capable of rapid dispersion, it is quite conceivable that this blowfly may migrate vertically to areas where temperatures fall within optimum ranges for its activity.

Of the three species studied, the relationship between seasonal prevalence and developmental rates is perhaps most striking for Eucalliphora lilaea. Adults generally disappear

from the Phoenix area by May 1, or before mean temperatures reach 80°F. (Figures 1, 3). They reappear in the fall, at about the time when mean temperatures descend to 80°. As mentioned previously, pupae held over from spring rearings, subjected to summer temperatures, were non-viable. Many of these had reached a late stage of development within the puparia. Pigment had been formed; adult structures appeared complete. Evidently, under natural conditions, there are large numbers of Eucalliphora literally halted in pre-imaginal stages of development at the onset of high temperatures. This phenomenon of heat injury to Eucalliphora and other cold-hardy species requires further investigation before its mechanism is clearly understood. Fraenkel and associates (16) (17) have done some preliminary work with Calliphora erythrocephala and Protophormia terrae-novae. Jefferson (32, p.112) believes that mitochondria are the first structures affected by heat; that heat liberates the mitochondrial lipids, disturbing enzymatic activity.

In order that Eucalliphora survive the summer, it would be necessary for larvae to descend in earth to a depth of one foot or more, since ground temperatures at lesser depths in the Phoenix area attain higher temperatures than 86°F. During five years of grill surveillance and trapping in this area, there was not a single adult of Eucalliphora observed during the summer months. How this species is able to maintain itself, recurring each fall, is a matter of speculation. Very little seems to be known about

its migratory habits. However, it appears to be readily attracted to the baited trap, and apparently is quite capable of wide dispersion. Members of the tribe Calliphorini, including Eucalliphora, were observed at higher altitudes in Arizona during summer months. Like Phormia, adults of this species may migrate vertically in the fall to areas where temperatures fall within optimum ranges for their activity.

There are no trapping records available for past seasons to indicate seasonal prevalence of Eucalliphora, Phormia and Musca in the Willamette Valley of Oregon. However, Eucalliphora appears to be present in Corvallis practically the year-round. Fly traps set during March and April often yield this species and other less prevalent representatives of Calliphorini almost exclusively. It is the impression of local federal personnel of the Division of Insects Affecting Man and Animals that Phormia is probably the predominant summer fly in this area, and that peaks of Musca populations (when they occur) are preceded by those of Phormia. The succession of initial peak populations appears to follow the same sequence wherever these three species coexist.

The following appear to be ranges of temperature in which developmental rates are linear: Musca, 65-95°F.; Phormia, 60-90°F.; and for Eucalliphora, 55-85°F. These estimates apply to field conditions such as those encountered in the Phoenix area. Range of mean temperatures from 65 to 95 degrees is coincident with highest observed fly densities (Figures 1 and 2). Range of mean temperatures from 65 to 95 degrees is also coincident with

highest observed prevalence of Musca domestica in the area (Figures 1 and 3). As discussed previously, absence of Phormia during summers is evidently not caused by retardation in development at high temperatures. However, it is also prevalent at temperatures within the range where linear relationship exists between temperature and developmental rates. The disappearance of Eucalliphora from the area occurs before mean temperatures attain 85°F. Its prevalence, likewise, is restricted to within ranges where the linear relationship is applicable.

Rearing insects at temperatures above and below this "linear range" and attempting to construct curves which describe the entire gamut has constituted several independent investigations. In the application of this concept to developmental rates of flies, it appears that more investigations need to be conducted before a truly symbolic curve can be derived (56, p.207). However, from the standpoint of the practical investigator charged with responsibility of control of muscoid flies in a given area, implications involved in the linear relationship within the optimum developmental range of temperatures for any given species will be sufficient to occupy his efforts. When retardation of development occurs, natural control factors are operating in his favor. Stress of competition from other coexistent species will serve to shift the focus of his attention to these other forms whose adaptations find better expression with shifts in levels of mean temperatures attendant with changing seasons.

The findings in this study emphasize the fact that a great deal of biological information is needed in order to attempt explanation of seasonal prevalence, for even three species of flies within the muscoid group. Fly density surveys, obtained by grill and trap methods, are expensive and time-consuming. Approximately 19,000 grill surveys are represented in Figure 2. Based on an average of 25 city blocks surveyed per man-day, this represents 760 man-days for obtaining grill data for just two years. The time required to trap, sort, identify and record species of trapped flies for only one year consumed at least 300 man-days (Figure 3). Yet, this extent of information is required before seasonal trends can be determined with any degree of accuracy.

In this particular study, quite a number of rather detailed statistical analyses were required in order to evaluate the data properly. Yet the time spent in analyzing these data is considered well justified, since it represents only a fraction of the time required in conducting the rearings and gathering the other pertinent biological information concerning the three species of flies studied.

Whether or not the amount of effort is justified in a practical field situation depends upon the extent of information desired. Laboratory research may be needed in order to clarify certain of the field problems. The integrated approach, combining both field and laboratory methods, is well summarized by Glen in his discussion of factors affecting insect abundance (19, pp.403,404).

SUMMARY AND CONCLUSIONS

Results from data obtained by grill and trap surveys over a period of five years at Phoenix, Arizona indicate that certain species of muscoid flies differ in their seasonal prevalence. Two main lines of evidence are considered in obtaining a better understanding of this seasonal prevalence for Musca domestica, Phormia regina and Eucalliphora lilaea. The first of these lines of evidence, temperature-developmental time relationships, was obtained by field rearings conducted at variable temperatures approximating field conditions. In addition, rearings of the same species were conducted under constant temperature conditions. Variable temperatures were characterized by sharp diurnal fluctuations. Constant temperature rearings were under thermostatically-controlled conditions with essentially no variance in temperatures. Linear regression methods were used in analyses of the data. These methods are applicable in testing developmental rates for conformation to linearity and for comparisons of rates for increments of the egg to adult periods as well as for total pre-imaginal periods. The following conclusions apply specifically to temperature-developmental time relationships:

1. The developmental rates of all three flies studied indicate a linear relationship throughout a temperature range in which they are prevalent in the study area.

2. Egg to adult development, for the three species studied, proceeds at parallel rates under constant and variable temperatures, the constant temperature rates being higher. Slower

development under variable temperature conditions may apparently be assigned to slower development in egg and larval stages.

3. Differences were insignificant in developmental rates for pupal periods of Musca domestica and Eucalliphora lilaea at constant and at variable temperatures.

4. Differences were less significant for developmental rates for pupal periods of Phormia regina than for egg to adult periods of the same species when reared at constant and at variable temperatures. Developmental rates for pupal periods of Phormia reared at variable temperatures were comparable to developmental rates for egg and larval periods under constant temperature conditions.

5. Slower rate of development at variable temperatures in the case of Eucalliphora lilaea is associated with wider range of linear relationship to temperature.

6. There were no significant differences in developmental rates for any of the three species studied between flies obtained at Phoenix, Arizona and at Corvallis, Oregon.

The second of these lines of evidence includes such biological factors as breeding habits, dispersal by flight, longevity and fecundity. These data were obtained from fly-breeding surveys, flight range tests and laboratory and field rearings. The following conslusions regarding seasonal prevalence for the species studied are based on both lines of evidence:

1. A rapid developmental rate extending into a high temperature range, versatility of larvae in utilizing many types of production media, favorable pre-oviposition and

longevity periods, and high fecundity are factors which serve to account for the predominance of Musca domestica at Phoenix, Arizona.

2. It is unlikely that summer temperatures in any of the metropolitan areas of the United States are sufficiently high so as to retard the development of Musca domestica. Under extremely warm and arid conditions, unavailability of suitably-moist media appears to be more of a critical factor in limiting housefly populations than high temperatures per se.

3. More rapid developmental rate at temperatures below 70°F. may account for the occurrence of initial peaks of Phormia regina before initial peaks of Musca domestica in Kansas, West Virginia and Michigan as well as in Arizona.

4. Selectivity in its utilization of types of production media may be a factor which limits the abundance of Phormia regina in metropolitan areas. Absence of immature stages of this species during summer seasons in southern areas is apparently not due to heat intolerance in these stages of development.

5. Mean temperatures above 85°F. are lethal to the development of Eucalliphora lilaea and Aldrichina grahami. Like Phormia, recurrence of these species each fall suggests vertical migration from higher altitudes.

6. With increasing temperatures, sequence of initial peaks of Eucalliphora lilaea, Phormia regina and Musca domestica occur in the order of species named. This sequence in initial peaks may be associated with developmental rates of the three species.

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APPENDIX

TABLE 5

Species Musca domestica Strain Phoenix

Rearings: Field X Laboratory ___ Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

91	88	85	82	79	76	70	67	61
(5)200	(5)200	(8)125	(7)143	(6)167	(9)111	(12)83	(19)53	(22)45
	(8)125	(6)167	(5)200	(8)125	(9)111	(10)100	(13)77	(20)50
	(6)167	(7)143				(14)71		
	(6)167	(6)167						
	(5)200	(5)200						
		(8)125						
		(5)200						
		(5)200						
		(5)200						

N 28

SS of x 2067.4286

Regression SS 55774.9766

Residual SS 1754.8814

b 5.1940 r .872

SP 10738.2858

$(\Sigma y)^2/N$ 549360.1420

$\sum\left(\frac{T^2}{N}\right)$ 607204.5300

Σy^2 622678.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	57844.3880	8		
Regression	55774.9766	1		
Deviations from Linearity	2069.4114	7	295.6302	.36
Error	1543.4700	19	81.4.3932	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.54 at 7 and 19 degrees of freedom

TABLE 6

Species Musca domestica Strain Phoenix

Rearings: Field X Laboratory ___ Period: Pupal

Hypothesis: That the regression of y on x is linear

91	88	85	82	79	76	67	64	61
(4)250	(4)250	(5)200	(6)167	(7)143	(7)143	(15)67	(15)67	(20)50
	(3)333	(5)200	(7)143	(8)125	(6)167	(9)111		
	(4)250	(3)333	(5)200		(4)250	(11)91		
	(3)333	(5)200	(6)167			(16)63		
	(5)200	(3)333	(5)200					
		(4)250						

N 28

SS of x 1950.4286

Regression SS 132138.3190

Residual SS 62684.3960

b 8.230939 r .823

SP 16053.8580

$(\Sigma y)^2/N$ 997921.2850

$\sum\left(\frac{T^2}{N}\right)$ 1147550.0000

Σy^2 1192744.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	149628.7150	8		
Regression	132138.3190	1		
Deviations from Linearity	17490.3960	7	2498.6280	1.05
Error	45194.0000	19	2378.6316	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.54 at 7 and 19 degrees of freedom

TABLE 8

Species Musca domestica Strain Corvallis

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(8)125	(9)111	(12)83	(15)67	(20)50	(28)36
(9)111	(10)100	(12)83	(15)67	(18)55	(27)37
(9)111	(10)100	(10)100	(13)77	(18)55	(26)38
(10)100	(11)91	(10)100	(13)77	(19)53	(24)42
(8)125	(11)91	(11)91	(13)77	(21)48	(28)36
(10)100	(10)100	(10)100	(14)71	(19)53	(25)40

N 36

SS of x 2256.00

Regression SS 24246.8156

Residual SS 1700.8233

b 3.2784 r .966

SP 7396.00

$(\Sigma y)^2/N$ 217933.3611

$\sum\left(\frac{T^2}{N}\right)$ 242435.8330

Σy^2 243881.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	24502.4719	5		
Regression	24246.8156	1		
Deviations from Linearity	255.6563	4	63.9141	1.33
Error	1445.1670	30	48.1722	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 9

Species Musca domestica Strain Corvallis

Rearings: Field ___ Laboratory X Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(4)250	(5)200	(5)200	(7)143	(11)91	(15)67
(5)200	(5)200	(5)200	(7)143	(9)111	(13)77
(4)250	(5)200	(6)167	(7)143	(7)143	(13)77
(5)200	(5)200	(5)200	(6)167	(8)125	(11)91
(4)250	(4)250	(6)167	(5)200	(12)83	(12)83
(4)250	(4)250	(5)200	(5)200	(9)111	(12)83

N 36
SS of x 2256.00
Regression SS 106851.3634
Residual SS 16760.2206
b 6.8821 r .929

SP 15526.00

$(\Sigma y)^2/N$ 990694.4160

$\sum\left(\frac{T^2}{N}\right)$ 1099558.6664

Σy^2 1114306.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	108864.2504	5		
Regression	106851.3634	1		
Deviations from Linearity	2012.8870	4	503.2218	1.02
Error	14747.3336	30	491.5778	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 10

Species Musca domestica Strain Corvallis

Rearings: Field ___ Laboratory X Period: Pupal

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(4)250	(4)250	(7)143	(8)125	(9)111	(13)77
(4)250	(5)200	(7)143	(8)125	(9)111	(14)71
(5)200	(5)200	(4)250	(6)167	(11)91	(13)77
(5)200	(6)167	(5)200	(7)143	(11)91	(13)77
(4)250	(7)143	(5)200	(8)125	(9)111	(16)63
(6)167	(6)167	(5)200	(9)111	(10)100	(13)77

N 36

SS of x 2256.00

Regression SS 94265.9082

Residual SS 27102.8418

b 6.4643 r .879

SP 14583.00

$(\Sigma y)^2/N$ 819930.2500

$\sum\left(\frac{T^2}{N}\right)$ 917053.1664

Σy^2 941299.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	97122.9164	5		
Regression	94265.9082	1		
Deviations from Linearity	2857.0082	4	714.2521	.88
Error	24245.8336	30	808.1945	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 12

Species Musca domestica Strain Phoenix

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(8)125	(9)111	(10)100	(15)67	(18)55	(28)36
(9)111	(10)100	(11)91	(14)71	(20)50	(30)33
(8)125	(10)100	(11)91	(13)77	(21)48	(29)35
(9)111	(10)100	(10)100	(14)71	(21)48	(27)37
(9)111	(11)91	(12)83	(13)77	(19)53	(28)36
(10)100	(11)91	(11)91	(15)67	(20)50	(27)37

N 36

SS of x 2256.00

Regression SS 26802.3830

Residual SS 1351.8393

b 3.4468 r .975

SP 7776.00

$(\Sigma y)^2/N$ 214677.7777

$\sum\left(\frac{T^2}{N}\right)$ 241731.0000

Σy^2 242832.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	27053.2223	5		
Regression	26802.3830	1		
Deviations from Linearity	250.8393	4	62.7098	1.71
Error	1101.0000	30	36.7000	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 13

Species Musca domestica Strain Phoenix

Rearings: Field ___ Laboratory X Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(5)200	(5)200	(5)200	(7)143	(10)100	(12)83
(4)250	(5)200	(5)200	(6)167	(11)91	(15)67
(4)250	(6)167	(5)200	(6)167	(9)111	(16)63
(4)250	(4)250	(5)200	(8)125	(9)111	(17)67
(5)200	(5)200	(6)167	(7)143	(8)125	(18)56
(5)200	(5)200	(6)167	(6)167	(10)100	(17)67

N 36

SS of x 2256.00

Regression SS 108495.5784

Residual SS 13378.3106

b 6.9348 r .946

SP 15645.00

$(\Sigma y)^2/N$ 887992.111

$\sum\left(\frac{T^2}{N}\right)$ 998457.0000

Σy^2 1009866.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	110464.8890	5		
Regression	108495.5784	1		
Deviations from Linearity	1969.3106	4	492.3276	1.29
Error	11409.0000	30	380.3000	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 14

Species Musca domestica Strain Phoenix

Rearings: Field ___ Laboratory X Period: Pupal

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(4)250	(4)250	(5)200	(8)125	(8)125	(16)63
(4)250	(5)200	(6)167	(8)125	(9)111	(15)67
(4)250	(4)250	(6)167	(7)143	(12)83	(13)77
(5)200	(6)167	(5)200	(6)167	(12)83	(10)100
(5)200	(6)167	(6)167	(6)167	(11)91	(10)100
(5)200	(6)167	(5)200	(9)111	(10)100	(10)100

N 36

SS of x 2256

Regression SS 95121.0997

Residual SS 20900.1233

b 6.4934 r .905

SP 14649.00

$(\Sigma y)^2/N$ 868002.7770

$\sum\left(\frac{T^2}{N}\right)$ 964674.0000

Σy^2 984024.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	96671.2230	5		
Regression	95121.0997	1		
Deviations from Linearity	1550.1233	4	387.5308	.60
Error	19350.0000	30	645.0000	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.54 at 4 and 30 degrees of freedom

TABLE 15a

Test of Hypothesis that the Regression Coefficients, for the Musca Rearings, are Equal

Strain	N	SS of x	SP	SS of y	b	Regression SS	df	Residual SS	df
Lab-Cor	36	2256.0000	7396.0000	25947.6389	3.2784	24246.8156	1	1700.8233	34
Lab-Phx	36	2256.0000	7776.0000	28154.2223	3.4468	26802.3830	1	1351.8393	34
Field	28	2106.9643	6334.8215	23468.1072	3.0066	19046.3424	1	4421.7648	26
						70095.5410	3	7474.4274	94
		6618.9643	21506.8215	77569.9684	3.2493	69881.5328	1		
					Difference	= 214.0082	2		

$$\frac{214.0082/2}{7474.4274/94} = \frac{107.0041}{79.5152} = 1.35$$

TABLE 15b

Test of Hypothesis that the Adjusted Means, for the Musca Rearings, are Equal

	d.f.	SS of x	SP	SS of y	Residual SS	df	Mean Square
Column	2	177.1457	78.1385	40.5916	1366.6560	2	683.3280
Error	97	6618.9643	21506.8215	77569.9694	7688.4366	96	80.0879
Total	99	6796.1100	21584.9600	77610.5600	9055.0926	98	

$$\frac{683.3280}{80.0879} = 8.53$$

TABLE 16a

Test of Hypothesis that the Regression Coefficients, for the Musca Lab. Rearings, are Equal

Strain	N	SS of x	SP	SS of y	b	Regression SS	Regression df	Residual SS	Residual df
Cor.	36	2256	7396	25947.6389	3.2784	24246.8156	1	1700.8233	34
Phx.	36	2256	7776	28154.2223	3.4468	26802.3830	1	1351.8393	34
						51049.1986	2	3052.6626	68
		4512	15172	54101.8612	3.3626	51017.1950	1		
					Difference -	32.0036	1		

$$\frac{32.0036}{44.8921} = .71$$

TABLE 16b

Test of Hypothesis that the Adjusted Means, for the Musca Lab. Rearings, are Equal

	d.f.	SS of x	SP	SS of y	Residual SS	Residual df	Mean Square
Column	1	0.0	0.0	6.1252	6.1252	1	6.1252
Error	70	4512.0	15172.00	54101.8612	3084.6662	69	4.4705
Total	71	4512.0	15172.00	54107.9864	3090.7914		

$$\frac{6.1252}{4.4705} = 1.37$$

TABLE 17

Derivation of Curves Shown in Figures 7,8 and 9

	Constant (Laboratory) Temperatures			Field (Variable) Temperatures		
	Egg to Adult	Egg plus larval	Pupal	Egg to Adult	Egg plus larval	Pupal
$\bar{y}_x$ =	77.5139 + 3.3426(x-77)	161.4722 + 6.9085(x-77)	153.0972 + 6.4787(x-77)	78.8214 - 3.0066(x -79.9643)	140.0714 + 5.1940(x -79.8571)	188.7857 + 8.2309(x -79.6429)
Temp.						
88	114.2837 (8.75*)	237.4657	224.3629	102.9815 (9.71)	182.3656	247.5721
84	100.9121 (9.91)	209.8317	198.4481	90.9551 (10.99)	161.5896	224.6485
80	87.5417 (11.42)	182.1977	172.5333	78.9287 (12.67)	140.8136	189.0796
75	70.8287 (14.12)	147.6552	140.1398	63.8958 (15.65)	114.8437	150.5705
70	54.1157 (18.48)	113.1127	107.7463	48.8628 (20.47)	88.8737	109.4160
65	37.4027 (26.74)	78.5702	75.3528	33.8298 (29.56)	62.9037	68.2615

* Parenthetical figures refer to the values for constructing the hyperbola shown in Figure 8.
For example, $\frac{1}{114.2837} \times 1000 = 8.75$

TABLE 21

Species Phormia regina Strain Phoenix

Rearings: Field X Laboratory ___ Period: Egg to adult

Hypothesis: That the regression of y on x is linear

88	85	82	79	73	67
(12)83	(10)100	(14)71	(14)71	(23)43	(26)38
(10)100	(11)91	(16)63	(17)59		(27)37
(12)83	(11)91		(14)71		(28)36
(11)91	(14)71		(19)53		(24)42
	(13)77				(24)41
	(15)67				
	(12)83				

N 23
SS of x 1335.9131
Regression SS 8090.4107
Residual SS 1581.4154
b 2.4609 r .914

SP 3287.5653

$(\Sigma y)^2/N$ 106080.1739

$\sum\left(\frac{T^2}{N}\right)$ 114402.3428

Σy^2 115752.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	8322.1689	5		
Regression	8090.4107	1		
Deviations from Linearity	231.7582	4	57.9395	.72
Error	1349.6572	17	79.3916	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.96 at 4 and 17 degrees of freedom

TABLE 22

Species Phormia regina Strain Phoenix

Rearings: Field x Laboratory ___ Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

91	88	85	82	79	76	70	64
(6)167	(6)167	(6)167	(6)167	(9)111	(8)125	(9)111	(13)77
	(5)200	(6)167	(9)111		(12)83	(14)71	(13)77
	(7)143	(7)143	(9)111			(13)77	
		(7)143				(9)111	
		(8)125					
		(6)167					
		(6)167					

N 23

SS of x 1443.9131

Regression SS 22128.4054

Residual SS 8833.4207

b 3.9009 r .845

SP 5632.5653

$(\Sigma y)^2/N$ 388180.1739

$\sum\left(\frac{T^2}{N}\right)$ 411385.4759

Σy^2 419142.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column				
	23205.3020	7		
Regression				
	22128.4054	1		
Deviations from Linearity				
	1076.8966	6	179.4827	.34
Error				
	7756.5241	15	517.1016	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.79 at 6 and 15 degrees of freedom

TABLE 23

Species Phormia regina Strain Phoenix

Rearings: Field X Laboratory ___ Period: Pupal

Hypothesis: That the regression of y on x is linear

91	88	85	82	79	67
(6)167	(5)200	(4)250	(5)200	(6)167	(13)77
(4)250		(4)250	(5)200	(5)200	(14)71
		(7)143	(7)143	(5)200	(15)67
		(5)200	(10)100	(10)100	(15)67
			(8)125	(9)111	(15)67
			(6)167		

N 23

SS of x 1277.2174

Regression SS 5215.3804

Residual SS 32707.2279

b 6.4062 r .785

SP 8182.0435

$(\Sigma y)^2/N$ 539325.3917

$\sum\left(\frac{T^2}{N}\right)$ 595727.7166

Σy^2 624448.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	5602.3249	5		
Regression	5215.3804	1		
Deviations from Linearity	3986.9445	4	996.7361	.59
Error	28720.2834	17	1689.4284	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.96 at 4 and 17 degrees of freedom

TABLE 25

Species Phormia regina Strain Corvallis

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(9)111	(11)91	(11)91	(14)71	(18)55	(24)42
(9)111	(10)100	(12)83	(14)71	(19)53	(23)43
(11)91	(9)111	(13)77	(14)71	(17)59	(23)43
(9)111	(10)100	(12)83	(15)67	(20)50	(24)42
(10)100	(10)100	(13)77	(13)77	(19)53	(24)42
(9)111	(11)91	(11)91	(13)77	(18)55	(22)45

N 36

SS of x 2256.00

Regression SS 18241.2345

Residual SS 1079.9878

b 2.8435 r .971

SP 6415.00

$(\Sigma y)^2/N$ 209458.7777

$\sum\left(\frac{T^2}{N}\right)$ 227818.0000

Σy^2 228780.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	18359.2223	5		
Regression	18241.2345	1		
Deviations from Linearity	117.9878	4	29.4970	.92
Error	962.0000	30	32.0667	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 26

Species Phormia regina Strain Corvallis

Rearings: Field ___ Laboratory X Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(4)250	(5)200	(5)200	(6)167	(10)100	(14)71
(5)200	(4)250	(5)200	(6)167	(12)83	(14)71
(5)200	(5)200	(6)167	(6)167	(9)111	(15)67
(5)200	(6)167	(7)143	(9)111	(11)91	(15)67
(6)167	(5)200	(6)167	(7)143	(10)100	(12)83
(4)250	(7)143	(7)143	(7)143	(10)100	(13)77

N 36

SS of x 2256

Regression SS 86804.9804

Residual SS 20020.9082

b 6.2030 r .901

SP 13994.00

$(\Sigma y)^2/N$ 799832.1114

$\sum\left(\frac{T^2}{N}\right)$ 888335.6664

Σy^2 906658.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	88503.5550	5		
Regression	86804.9804	1		
Deviations from Linearity	1698.5746	4	424.6437	.70
Error	18322.3336	30	610.7445	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 27

Species Phormia regina Strain Corvallis

Rearings: Field ___ Laboratory X Period: Pupal

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(5)200	(6)167	(6)167	(8)125	(8)125	(10)100
(4)250	(6)167	(7)143	(8)125	(7)143	(9)111
(6)167	(4)250	(7)143	(8)125	(8)125	(8)125
(4)250	(5)200	(5)200	(6)167	(9)111	(9)111
(4)250	(5)200	(5)200	(6)167	(9)111	(12)83
(5)200	(4)250	(6)167	(6)167	(8)125	(9)111

N 36

SS of x 2256

Regression SS 59245.0005

Residual SS 22094.5553

b 5.1246 r .850

SP 11561.00

$(\Sigma y)^2/N$ 943488.4442

$\sum\left(\frac{T^2}{N}\right)$ 1003917.0000

Σy^2 1024828.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	60428.5558	5		
Regression	59245.0005	1		
Deviations from Linearity	1183.5553	4	295.8888	.42
Error	20911.0000	30	697.0333	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.69 at 4 and 30 degrees of freedom

TABLE 29

Species Phormia regina Strain Phoenix

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(10)100	(10)100	(10)100	(12)83	(15)67	(24)42
(9)111	(11)91	(10)100	(14)71	(17)59	(24)42
(11)91	(10)100	(10)100	(14)71	(19)53	(25)40
(8)125	(10)100	(12)83	(13)77	(18)55	(24)42

N 24

SS of x 1504.00

Regression SS 12575.6656

Residual SS 1525.2928

b 2.8916 r .943

SP 4349.00

$(\Sigma y)^2/N$ 150892.0416

$\sum\left(\frac{T^2}{N}\right)$ 163853.7500

Σy^2 164993.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	12961.7084	5		
Regression	12575.6656	1		
Deviations from Linearity	386.0428	4	96.5107	1.52
Error	1139.2500	18	63.2917	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.93 at 4 and 18 degrees of freedom

TABLE 30

Species Phormia regina Strain Phoenix

Rearings: Field ___ Laboratory X Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(6)167	(6)167	(5)200	(7)143	(8)125	(14)71
(5)200	(6)167	(6)167	(7)143	(9)111	(16)63
(5)200	(5)200	(5)200	(8)125	(12)83	(15)67
(4)250	(5)200	(6)167	(6)167	(8)125	(15)67

N 24

SS of x 1504

Regression SS 52040.8305

Residual SS 10238.1283

b 5.8823 r .914

SP 8847.00

$(\Sigma y)^2/N$ 532526.0412

$\sum\left(\frac{T^2}{N}\right)$ 587011.2500

Σy^2 594805.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	54485.2088	5		
Regression	52040.8305	1		
Deviations from Linearity	2444.3783	4	611.0946	1.41
Error	7793.7500	18	432.9861	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.93 at 4 and 18 degrees of freedom

TABLE 31

Species Phormia regina Strain Phoenix

Rearings: Field ___ Laboratory X Period: Pupal

Hypothesis: That the regression of y on x is linear

88	84	80	75	70	65
(4)250	(4)250	(5)200	(5)200	(7)143	(10)100
(4)250	(5)200	(4)250	(7)143	(8)125	(8)125
(6)167	(5)200	(5)200	(6)167	(7)143	(10)100
(4)250	(5)200	(6)167	(7)143	(10)100	(9)111

N 24
SS of x 1504
Regression SS 47004.2979
Residual SS 13374.6609
b 5.5904 r .882

SP 8408.00

$(\Sigma y)^2/N$ 731155.0412

$\sum\left(\frac{T^2}{N}\right)$ 779257.2500

Σy^2 791534.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	48102.2088	5		
Regression	47004.2979	1		
Deviations from Linearity	1097.9109	4	274.4777	.40
Error	12276.7500	18	682.0417	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.93 at 4 and 18 degrees of freedom

TABLE 32a

Test of Hypothesis that the Regression Coefficients, for the Phormia rearings, are Equal

Strain	N	SS of x	SP	SS of y	b	Regression SS	Regression df	Residual SS	Residual df
Lab-Cor.	36	2256.0000	6415.0000	19321.2223	2.8435	18241.2345	1	1079.9878	34
Lab-Phx.	24	1504.0000	4349.0000	14100.9584	2.8916	12575.6656	1	1525.2928	22
Field	23	1335.9131	3187.5653	9671.8261	2.4609	8090.4107	1	1581.4154	21
						38907.8108	3	4186.6960	73
		5095.9131	14051.5653	43094.0068	2.7574	38746.0467	1		
					Difference	- 161.2641	2		

$$\frac{161.2641/2}{4186.6960/73} = 1.41$$

TABLE 32b

Test of Hypothesis that the Adjusted Means, for the Phormia Rearings, are Equal

	d.f.	SS of x	SP	SS of y	Residual SS	Residual df	Mean Square
Column	2	1682.9545	-442.7700	-40102.2115	-28676.2601	2	14338.1301
Error	80	5095.9131	14051.5653	43094.0068	4347.9601	79	55.0374
Total	82	6778.8676	13608.7953	2991.7953	-24328.3000	81	

$$\frac{14338.1301}{55.0374} = 260.51$$

TABLE 33a

Test of Hypothesis that the Regression Coefficients, for the Phormia Lab. Rearings, are Equal

Strain	N	SS of x	SP	SS of y	b	Regression SS	df	Residual SS	df
Cor.	36	2256.00	6415.00	19321.2223	2.8435	18241.2345	1	1079.9878	34
Phx.	24	1504.00	4349.00	14100.9584	2.8916	12575.6656	1	1525.2928	22
						30816.9001	2	2605.2806	56
		3760.00	10764.00	33422.1807	2.8628	30814.8127	1		
						2.0874	1		

$$\frac{2.0874/1}{2605.2806/56} = .04$$

TABLE 33b

Test of Hypothesis that the Adjusted Means, for the Phormia Lab. Rearings, are Equal

	d.f.	SS of x	SP	SS of y	Residual SS	df	Mean Square
Column	1	0.0	0.0	130.8029	130.8029	1	130.8029
Error	58	3760.0	10764.00	33422.1807	2607.3680	57	45.7433
Total	59	3760.0	10764.00	33552.9836	2738.1709		

$$\frac{130.8029}{45.7433} = 2.85$$

TABLE 34

Derivation of Curves Shown in Figures 10,11 and 12

	Constant (Laboratory) Temperatures			Field (Variable) Temperatures		
	Egg to Adult	Egg plus larval	Pupal	Egg to Adult	Egg plus larval	Pupal
$\bar{y}x$ =	77.4833 + 2.756(x-77)	149.0167 + 6.0747(x-77)	166.95 + 5.3109(x-77)	67.9130 + 2.4609(x -79.7826)	129.9130 + 3.9009(x -79.7826)	153.1304 + 6.4061(x -79.6522)
Temp.						
88	107.7993 (9.28)	215.8384	225.3699	88.1352 (11.34)	161.9683	206.6072
84	96.7753 (10.33)	191.5396	204.1263	78.2916 (12.77)	146.3647	180.9828
80	85.7513 (11.66)	167.2408	182.8827	68.4480 (14.61)	130.7611	155.3584
75	71.9713 (13.89)	136.8673	156.3282	56.1435 (17.81)	111.2566	123.3279
70	58.1913 (17.18)	106.4938	129.7737	43.8390 (22.81)	91.7521	91.2974
65	44.4113 (22.52)	76.1203	103.2192	31.4345 (31.71)	72.2476	59.2669

TABLE 38

Species Eucalliphora lilaea Strain Phoenix

Rearings: Field X Laboratory ___ Period: Egg to adult

Hypothesis: That the regression of y on x is linear

85	82	79	76	73	67	64	61
(13)77	(17)59	(16)63	(17)59	(18)55	(22)45	(28)36	(32)31
(15)67		(17)59	(18)55		(27)37	(25)40	(31)32
(13)77					(28)36	(28)36	
					(22)45		
					(26)38		
					(24)42		
					(24)42		
					(26)38		

N 22
SS of x 1363.0910
Regression SS 3895.3182
Residual SS 278.0000
b 1.6905 r .961

SP 2304.2728
$(\Sigma y)^2/N$ 51943.6818
$\sum\left(\frac{T^2}{N}\right)$ 55933.2916
Σy^2 56117.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	3989.6098	7		
Regression	3895.3182	1	15.7153	1.20
Deviations from Linearity	94.2916	6	13.1220	
Error	183.7084	14		

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 4.46 at 6 and 14 degrees of freedom

TABLE 39

Species Eucalliphora lilaea Strain Phoenix

Rearings: Field X Laboratory ___ Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

88	85	79	76	70	67	64	61
(7)143	(8)125	(7)143	(7)143	(8)125	(13)77	(10)100	(15)67
(7)143	(7)143	(10)100	(8)125	(11)91	(15)67		(15)67
		(9)111	(9)111	(11)91	(10)100		(13)77
			(9)111		(13)77		
					(12)83		
					(10)100		
					(13)77		

N 25

SS of x 1668.24

Regression SS 12179.3160

Residual SS 4761.2790

b 2.7020 r .838

SP 4507.56

$(\Sigma y)^2/N$ 269776.36

$\sum\left(\frac{T^2}{N}\right)$ 283086.66

Σy^2 286717.90

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	13310.3000	7		
Regression	12179.3610	1		
Deviations from Linearity	1130.9390	6	188.4898	.88
Error	3630.34	17	213.5494	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 4.46 at 6 and 17 degrees of freedom

TABLE 40

Species Eucalliphora lilaea Strain Phoenix

Rearings: Field X Laboratory ___ Period: Pupal

Hypothesis: That the regression of y on x is linear

85	82	79	76	70	67	64	61
(10)100	(6)167	(9)111	(8)125	(12)83	(13)77	(14)71	(15)67
(7)143		(9)111			(15)67	(12)83	(17)59
(6)167		(8)125				(15)67	(18)55
		(9)111				(13)77	
						(15)67	
						(14)71	
						(14)71	

N 22

SS of x ___

Regression SS ___

Residual SS ___

b ___ r ___

SP 5659.3637

$(\Sigma y)^2/N$ 195710.2272

$\sum\left(\frac{T^2}{N}\right)$ 216886.6190

Σy^2 219661.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	21176.3918	7		
Regression	19226.8265	1		
Deviations from Linearity	1949.5653	6	324.9276	1.64
Error	2774.3810	14	198.1701	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 4.46 at 6 and 14 degrees of freedom

TABLE 42

Species Eucalliphora Strain Corvallis

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

84	80	75	70	65
(16)63	(14)71	(16)63	(18)56	(21)48
(16)63	(14)71	(17)59	(18)56	(21)48
(14)71	(15)67	(13)77	(20)50	(20)50
(14)71	(13)77	(15)67	(19)53	(22)45

N 20

SS of x 923.20

Regression SS 1315.9065

Residual SS 632.2935

b ____ r ____

SP 1102.2

$(\Sigma y)^2/N$ 75153.8000

$\sum\left(\frac{T^2}{N}\right)$ 76770.5000

Σy^2 77102.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	1616.7000	4		
Regression	1315.9065	1		
Deviations from Linearity	300.7935	3	100.2645	4.54
Error	331.5000	15	22.1000	

Conclusion: ~~Reject~~ / Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is ~~less~~ more than 3.29 at 3 and 15 degrees of freedom

TABLE 43

Species Eucalliphora lilaea Strain Corvallis

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

80	75	70	65
(14)71	(16)63	(18)56	(21)48
(14)71	(17)59	(18)56	(21)48
(15)67	(13)77	(20)56	(20)50
(13)77	(15)67	(19)53	(22)45

N 16
SS of x 500.00
Regression SS 1411.20
Residual SS 310.55
b 1.6800 r .905

SP 840.0
$(\Sigma y)^2/N$ 57360.2500
$\sum\left(\frac{T^2}{N}\right)$ 58814.5000
Σy^2 59082.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	1454.2500	3		
Regression	1411.2000	1		
Deviations from Linearity	43.0500	2	21.5250	.97
Error	267.5000	12	22.2917	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 3.89 at 2 and 12 degrees of freedom

TABLE 45

Species Eucalliphora Strain Combined

Rearings: Field ___ Laboratory X Period: Egg to adult

Hypothesis: That the regression of y on x is linear

80	75	70	65
(14)71	(15)67	(18)56	(22)45
(14)71	(16)63	(19)53	(20)50
(13)77	(15)67	(20)50	(23)43
(14)71	(17)59	(20)50	(23)44
(14)71	(16)63	(18)56	(21)48
(14)71	(17)59	(18)56	(21)48
(15)67	(13)77	(20)50	(20)50
(13)77	(15)67	(19)53	(22)45

N 32

SS of x 1000.00

Regression SS 3124.0563

Residual SS 473.41255

b 1.7675 r .932

SP 1767.50

$(\Sigma y)^2/N$ 112219.5312

$\sum\left(\frac{T^2}{N}\right)$ 115395.6250

Σy^2 115817.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	3176.0938	3		
Regression	3124.0563	1		
Deviations from Linearity	52.0375	2	26.0188	1.73
Error	421.3750	28	15.0491	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 3.34 at 2 and 28 degrees of freedom

TABLE 46

Species Eucalliphora lilaea Strain Combined

Rearings: Field ___ Laboratory X Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

84	80	75	70	65
(5)200	(6)167	(7)143	(7)143	(10)100
(6)167	(5)200	(6)167	(8)125	(8)125
(7)143	(6)167	(5)200	(8)125	(8)125
(9)111	(6)167	(5)200	(10)100	(11)91
(7)143	(5)200	(7)143	(6)167	(10)100
(7)143	(5)200	(6)167	(8)125	(7)143
(5)200	(5)200	(6)167	(9)111	(9)111
(9)111	(6)167	(6)167	(11)91	(10)100

N 40

SS of x 1846.4

Regression SS 16992.8953

Residual SS 32259.0047

b ——— r ———

SP 5601.4

$(\Sigma y)^2/N$ 876752.1000

$\sum\left(\frac{T^2}{N}\right)$ 905882.2500

Σy^2 926004.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	29130.1500	4		
Regression	16992.8953	1		
Deviations from Linearity	12137.2547	3	4045.7516	7.04
Error	20121.7750	35	574.9078	

Conclusion: Reject the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is more than 2.87 at 3 and 35 degrees of freedom

TABLE 47

Species Eucalliphora lilaea Strain Combined

Rearings: Field ___ Laboratory X Period: Egg plus larval

Hypothesis: That the regression of y on x is linear

80	75	70	65
(6)167	(7)143	(7)143	(10)100
(5)200	(6)167	(8)125	(8)125
(6)167	(5)200	(8)125	(8)125
(6)167	(5)200	(10)100	(11)91
(5)200	(7)143	(6)167	(10)100
(5)200	(6)167	(8)125	(7)143
(5)200	(6)167	(9)111	(9)111
(6)167	(6)167	(11)91	(10)100

N 32

SS of x 1000.00

Regression SS 27196.2250

Residual SS 13441.7750

b 5.2150 r .817

SP 5215.00

$(\Sigma y)^2/N$ 691488.0000

$\sum\left(\frac{T^2}{N}\right)$ 720441.7500

Σy^2 732126.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	28953.7500	3		
Regression	27196.2250	1		
Deviations from Linearity	1757.5250	2	878.7625	2.11
Error	11684.2500	28	417.2866	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 3.34 at 2 and 28 degrees of freedom

TABLE 48

Species Eucalliphora lilaea Strain Combined

Rearings: Field ___ Laboratory X Period: Pupal

Hypothesis: That the regression of y on x is linear

84	80	75	70	65
(7)143	(9)111	(8)125	(12)83	(12)83
(9)111	(9)111	(10)100	(11)91	(13)77
(9)111	(8)125	(9)111	(11)91	(14)71
(6)167	(8)125	(11)91	(9)111	(13)77
(11)91	(8)125	(9)111	(11)91	(11)91
(10)100	(9)111	(11)91	(10)100	(13)77
(7)143	(9)111	(8)125	(12)83	(12)83
(5)200	(7)143	(10)100	(9)111	(11)91

N 40
SS of x 1846.40
Regression SS 13311.1990
Residual SS 13145.5760
b 2.6850 r .709

SP 4957.6
$(\Sigma y)^2/N$ 460746.2250
$\sum\left(\frac{T^2}{N}\right)$ 474092.1250
Σy^2 487203.0000

Analysis of Variance

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	F
Column	13345.9000	4		
Regression	13311.1990	1		
Deviations from Linearity	34.7010	3	11.5670	.029
Error	13110.8750	35	374.5964	

Conclusion: Accept the hypothesis that the regression of y on x is linear, since at the 5% level of significance, F is less than 2.87 at 3 and 35 degrees of freedom

TABLE 49a

Test of Hypothesis that the Regression Coefficients, for the Eucalliphora Rearings, are Equal

Strain	N	SS of x	SP	SS of y	b	Regression SS	Regression d.f.	Residual SS	Residual d.f.
Lab.*	32*	1000.0000	1767.5000	3597.4688	1.7675	3124.0563	1	473.4126	30
Field	22	1363.0910	2304.2728	4173.3182	1.6905	3895.3182	1	278.0000	20
						7019.3745	2	751.4126	50
		2363.0910	4071.7728	7770.7870		7015.9523	1		
						3.4222	1		

$$\frac{3.4222/1}{151.4126/50} = 0.23$$

TABLE 49b

Test of Hypothesis that the Adjusted Means, for the Eucalliphora Rearings, are Equal

d.f.		SS of x	SP	SS of y	Residual SS	Residual d.f.	Mean Square
Column	1	16.8346	157.4498	1472.5464	973.0017	1	973.0017
Error	52	2363.0910	4071.7728	7770.7870	754.8347	51	14.8007
Total	53	2379.9256	4229.2226	9243.3334	1727.8364	52	

$$\frac{973.0017}{14.8007} = 65.74$$

*Through a limited temperature range, of from 65 to 80 degrees.

TABLE 50

Derivation of Curves Shown in Figures 13,14 and 15

	Constant (Laboratory) Temperatures			Field (Variable) Temperatures		
	Egg to Adult	Egg plus larval	Pupal	Egg to Adult	Egg plus larval	Pupal
$\bar{y}x$ =	59.2188 + 1.7675(x -72.50)	147.0 + 5.215 (x-72.5)	107.3250 + 2.6850(x -71.3636)	48.5909 + 1.6905(x -71.3636)	103.88 + 2.702 (x-72.52)	94.3182 + 3.3973(x -71.0909)
Temp. 88	-	-	-	-	-	-
84	-	-	132.0270	69.9527 (14.30)	134.90	138.1743
80	72.4751 (13.80)	186.1125	121.2870	63.1907 (15.83)	124.09	124.5851
75	63.6376 (15.71)	160.0375	107.8620	54.7382 (18.27)	110.58	107.5986
70	54.8000 (18.25)	133.9625	94.4370	46.2857 (21.60)	97.0710	90.6121
65	45.9625 (21.76)	107.8875	81.0120	37.8332 (26.43)	83.5610	73.6256

TABLE 51

Comparison of developmental rates for Musca, Phormia and Eucalliphora

	Musca domestica			Phormia regina			Eucalliphora lilaea		
Lab. Rearings	Corv.	Phx.	Pooled b	Corv.	Phx.	Pooled b	Corv.	Phx.	Pooled b
Egg + larval	6.8821 (.929)	6.9348 (.946)		6.2030 (.901)	5.8823 (.914)				5.2150 (.817)
Pupal	6.4641 (.879)	6.4934 (.905)		5.1246 (.850)	5.5904 (.882)				2.6850 (.709)
Egg to adult	3.2752 (.976)	3.3213 (.966)	3.2983	2.8435 (.971)	2.8916 (.943)	2.8628	1.6800* (.905)	1.855* (.961)	1.7675* (.932)
Field Rearings									
Egg + larval		5.1940 (.872)			3.9009 (.845)			2.7020 (.838)	
Pupal		8.2309 (.823)			6.4062 (.785)			3.3973 (.896)	
Egg to adult		3.0066 (.901)	3.0066		2.4609 (.914)	2.4609		1.6905 (.961)	1.6905 (.961)
Mean Regression Coefficient			3.2324			2.7574			1.7262

$\bar{y}x = 88.1774 - 3.2324(x - 80.86)$

$\bar{y}x = 748313 + 2.7574(x - 77.7711)$

$\bar{y}x = 548888 + 1.7262(x - 72.0185)$

*Limited temperature range, 65-80°

TABLE 52a

Test of Hypothesis that the Adjusted Means for the Pupal Periods of *Musca domestica* are Equal

	d.f.	SS of x	SP	SS of y	Residual SS	Residual d.f.
Column	2	140.8114	1901.4820	26019.5020	5157.9135	2
Error	97	6462.4286	45285.8580	433212.6880	115869.3500	96
Total	99	6603.2400	47187.3400	458232.1900	121027.2635	

$$\frac{5157.9135/2}{115869.3500/96} = 2.14$$

TABLE 52b

Test of Hypothesis that the Adjusted Means for the Pupal Periods of *Eucalliphora lilaea* are Equal

Column	1	195.2650	684.7461	2401.2267	433.0410	1
Error	60	3512.2182	10616.9637	50407.5478	18313.8931	59
Total	61	3707.4832	11301.7098	52808.7745	18357.1972	60

$$\frac{433.0410/1}{18313.8931/59} = 1.40$$

TABLE 52c

Test of Hypothesis that the Adjusted Means for the Pupal Periods of *Phormia regina* are Equal

Column	2	116.9513	-609.5368	5480.6831	15637.0503	2
Error	80	5037.2174	28151.0435	226841.1229	69515.6026	79
Total	82	5154.1687	27541.5067	232321.7960	85152.6529	81

$$\frac{15637.0503/2}{69515.6026/79} = 8.88$$

TABLE 52d

Test of Hypothesis that the Adjusted Means for the Larval Periods (lab) and Pupal Periods (Field) of *Phormia* are Equal

Column	2	116.9513	181.4023	281.5093	2426.8505	2
Error	80	5037.2174	31203.0435	254227.4557	63163.6887	79
Total	82	5154.1687	31204.4458	254508.9650	65590.5392	

$$\frac{2426.8505/2}{63163.6887/79} = 1.52$$