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## EFFECT OF CONSTANT TEMPERATURE ENVIRONMENTS ON THE EGG STAGE OF THREE SPECIES OF HAWAIIAN FRUIT FLIES<sup>1</sup>

P. S. MESSENGER

Department of Biological Control, University of California Agricultural Experiment Station

N. E. FLITTERS<sup>2</sup>

Entomology Research Branch, Agricultural Research Service,  
U. S. Department of Agriculture,  
Honolulu, T. H.<sup>3</sup>

To facilitate the analysis and evaluation of data derived from an intensive bioclimatic study of three species of tephritid fruit flies in Hawaii (Flitters and Messenger 1953), information about the effects of constant temperatures upon the duration of development of the different stages of these insects is required. These tephritids, the oriental fruit fly, *Dacus dorsalis* Hendel, the melon fly, *D. cucurbitae* Coq., and the Mediterranean fruit fly, *Ceratitis capitata* (Wied.), are tropical to subtropical in distribution, and a major factor in this distribution appears to be the temperature of their surroundings. These insects do not normally exist in the continental United States, and the Hawaiian bioclimatic studies had the objective of determining their potential distribution on the mainland should they ever gain entry and become established there. From that standpoint the effects of relatively extreme temperatures are needed, since such temperatures are encountered regularly in the climates of the continental United States. Winter temperatures frequently drop to near freezing, in those climatic sites studied, and fruit fly development and activity are interrupted thereby. Also summer conditions show occasional high temperatures at which development is suppressed and recovery reduced. Hence it is desirable to know the temperature thresholds and

upper limits for development and the mortality relationships existing at such conditions.

To provide this information a series of studies of the effects of both constant and regularly fluctuating temperatures upon the development of the different immature stages of these insects was carried out. The present paper deals with the effects of constant temperature environments upon the egg stage. Studies of the remaining stages, and of the effects of fluctuating temperatures will be reported later.

Numerous reports concerning the life history of the Mediterranean fruit fly indicate that, in general, the duration of the egg stage ranges from 2 to 4 days in temperate summers or in warm tropical regions (Newman 1913; Back and Pemberton 1915, 1918) and from as much as 14 to 19 days in cooler conditions (Newman 1913). Eggs held continuously in mild cold storage at 59°–62°<sup>4</sup> hatched in 5 to 7 days; at 54°–57° they hatched in 7 to 14 days, and at 48°–53° in 18 to 27 days (Back and Pemberton 1918).

McBride (1935) stated that development proceeded normally at temperatures between 70° and 90°, with the optimum for this stage occurring at 90° (greatest hatch in shortest time, 38 hours). Growth was retarded considerably at temperatures below 65°; at 55° the egg stage lasted 15 days, and none hatched below 52°. Keck (1933) indicated that at a constant temperature of 52.5° hatch occurred in 20 days.

The melon fly egg stage has been studied in some detail in Hawaii and the Orient. Back and Pemberton (1914), in Hawaii, observed that at a mean temperature of 79° eggs hatched in

<sup>1</sup>Paper No. 975, University of California Citrus Experiment Station, Riverside, California.

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<sup>2</sup>Present address: Pink Bollworm Research Center, P. O. Box 1033, Brownsville, Texas.

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<sup>4</sup>All temperatures given in this paper are in degrees Fahrenheit unless otherwise designated.

from 26 to 35 hours, while at a mean temperature of 73.6° hatching occurred after 52–54 hours. Kato (1928) and Koidsumi and Shibata (1935) reported 6- and 10-hour incubation periods, respectively, for melon fly eggs during the summer season on Formosa—periods which seem rather short in comparison with others cited herein. Koreishi (1937), on Formosa, and Renjhen (1949), in India, confirmed the earlier Hawaiian work, reporting that under natural conditions in these two areas the egg stage lasted about 24 hours in summer and from 4 to 9 days in winter.

Shibata (1936b) conducted constant temperature studies on melon fly eggs and reported that the favorable temperatures for hatching occurred between 60° and 90°. At 53.6° development required 190 hours, while at 51.8° no hatching occurred. At high temperatures, development required 22 hours at 95.0°, while no response was noted at 96.8°. The shortest developmental time, 20.1 hours, occurred between 89° and 91°. The number of eggs hatching in each sample reached a maximum value between the limits 60.8°–91.4°. Above and below these limits the proportion of eggs that hatched dropped off rapidly. Keck (1951), in Hawaii, reported the effects of constant temperature conditions on melon fly eggs, finding that swiftest development occurred at 90° (17 hours minimum, 19 hours mean), slightly retarded development at 95° (19.7 hours, mean) and no hatch at 100°. Only a few eggs hatched at 55° (no time of development given).

Oriental fruit fly eggs, under natural conditions in Formosa, hatched in from 24 hours in summer to 20 days in winter (Maki 1921). With temperatures below 50° no hatch was observed. Under constant temperature conditions in Formosa (Shibata 1936a) no hatch occurred at 51.8° or below, or at 102.2° or above. Egg development required at least 10.5 days at 53.6°, the lowest temperature at which hatching was noted, and 35.8 hours at 95°, the highest temperature at which hatching occurred. Swiftest development occurred at 89.6°, taking 26 hours. Flitters (1950), in Hawaii, observed no hatch at 54.5°, hatch in 7.5 days at 59°, and again no hatch at 99.5°.

To ascertain as accurately as possible the effects of extremes in temperature upon the developmental stages of these three species of fruit flies, hatching time and the percent hatching were observed at various constant temperatures between 52° and 98°. Emphasis was placed upon temperatures near the threshold of development, although sufficient data were collected to permit the construction of the entire temperature-development curve.

A major virtue of the work in Honolulu was the availability of the three species of fruit flies in large numbers and the consequent advantage of conducting experiments upon them simultane-

ously. This facilitated direct comparison of species.

#### MATERIALS AND METHODS

Eggs were collected in the insectary by exposing thin circular sections of orange peel or cucumber peel, fastened to glass plates with paraffin, for 1-hour intervals in cages containing gravid female flies (Baker 1945). The eggs of each species (for description of egg characters, see Hardy 1949) were removed from the sections with a moistened camel's-hair brush, collected in water, and mixed well. Approximately 1 to 200 eggs of a given species were placed upon each of two moistened squares of blackened filter paper. These squares were then fastened to the inside walls of small glass vials and adjusted to touch a wad of water-soaked cotton at the bottom of the vial. This ensured a constantly moistened condition of the filter paper and maintained the eggs in a saturated environment. To reduce contamination by molds and fungi the water used in the vials contained 0.1 percent cupric chloride. The vials were closed tightly with one-hole rubber stoppers fitted with a 2-inch length of glass tubing for air access. Each set of vials, containing a total of between 200 and 400 eggs, was then submerged in a constant temperature water bath. In certain instances, where the temperatures used were near, at, or just beyond the developmental limits and only a few eggs of the sample were expected to hatch, more than two vials were used in the set. The number of eggs in such samples ranged from 500 to over 1,000. Temperatures were maintained with electronic relays controlled by metastatic mercury thermo-regulators to within plus or minus 0.1 degree F.

Preliminary screening tests were made at each temperature studied in order to indicate the approximate time of first hatch. This was accomplished by withdrawing the vials from the bath at 4-hour intervals throughout the incubation period and observing for hatched eggs under the dissecting scope at 18 power magnification. At low temperatures, readings were begun only about 24 hours before the estimated time of hatching.

With this preliminary information on the time of first hatch, more accurate tests were made in which the new set of tubes was left in the bath for almost the entire incubation period. Several hours prior to first hatch, hourly readings were begun and were continued until the number hatching attained a maximum value. The average time required to make each count was about 2 minutes at each reading.

#### RESULTS

The temperatures studied, the number of eggs incubated, the incubation period, the hatching range, the median hatching time, and the percentage hatching are recorded in Tables I to III.

The incubation period was computed as the elapsed time from the midpoint of the ovipositional interval to the last hourly reading prior to first hatch (see also Shaw and Starr 1946). The hatching range was computed as the elapsed time between the first hatch and maximum hatch. The median hatching time was estimated from the hatching data by the method of probits (Bliss 1937).

Developmental rates for eggs of *Dacus dorsalis* were derived from the hatching data of Table I according to the method of Shelford (1927) and are shown plotted in figure 1. Plots of the other two species considered here have approximately identical shapes and therefore are not presented. The curves of figure 1 were fitted by eye. While curve-fitting by formula is intriguing and eventually useful in elucidating fundamental issues of

of fully developed embryos were usually noted prior to the time of eclosion whether the latter actually occurred or not. When first noticeable—from 4 to 24 hours before actual hatch, the length of time depending upon the temperature—these movements were pulsations restricted to slight elongations and contractions in which the fully extended embryo seldom touched both ends of the shell at one time. With approach of eclosion these pulsations became more vigorous both in frequency and extent and the embryo filled the entire shell. The mouth parts, previously moved at random about the anterior end of the shell, were forced actively against the chorion. At eclosion the shell split anteriorly and the emerging larva worked its way out gradually, usually splitting the shell completely from end to end in the process.

TABLE I  
EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON EGG DEVELOPMENT OF THE  
ORIENTAL FRUIT FLY, *Dacus dorsalis* HENDEL

TEMPER- TURE (°F.)	EGGS INCUBATED (No.)	INCUBATION PERIOD (Hrs.)	HATCHING RANGE (Hrs.)	MEDIAN HATCHING TIME (Hrs.) <sup>a</sup>	PERCENT HATCH
54.5	1550	....	..	.....	0
55.0	1042	263.0	..	264.0	0.1
56.0	229	232.0	14	239.0±1.37	2.2
57.0	281	170.5	54	193.0±2.10	13.9
58.0	303	148.0	50	176.5±2.35	14.8
60.0	413	121.3	44	136.5±0.64	52.1
62.5	191	95.5	22	103.0±0.29	68.6
65.0	429	74.0	17	80.0±0.12	81.1
67.5	261	62.5	13	65.5±0.15	73.2
70.0	225	51.5	12	54.1±0.12	83.5
75.0	287	38.0	9	40.1±0.07	70.0
80.0	409	30.5	10	32.6±0.05	77.0
85.0	227	27.0	6	28.5±0.06	70.0
87.5	200	25.0	7	27.0±0.14	74.0
90.0	200	24.0	8	26.3±0.17	77.0
92.5	304	23.5	4	25.7±0.04	78.3
95.0	474	25.0	12	27.1±0.11	56.8
96.0	481	26.5	16	29.7±0.24	18.7
97.0	1593	29.3	73	33.6±0.39	7.8
97.5	1220	34.3	28	43.8	0.4
98.0	1856	....	..	.....	0

<sup>a</sup>Median hatching time includes standard error estimated from regression curves.

growth, the objectives of the present work are equally as well satisfied by eye-fitted curves.

#### DISCUSSION

Basic assumptions in this work are (1) that the development of eggs of fruit flies is terminated by hatching, (2) that no hatch means that development did not go to completion, and (3) that variations in hatching time are due to similar variations in rate of development. In a strict sense, development may not necessarily be indicated by hatching, since under certain environmental conditions there may be a period of dormancy or quiescence between the time of completed development and eclosion. Movements

The above description applies to eclosion at medial temperatures. As such, eclosion usually involved about 3 to 4 minutes from the first signs of shell splitting to full emergence of the larva. At extremes of temperature the process was considerably slowed. At low temperatures within 3 or 4 degrees of the threshold of egg hatch, slight movements of the embryo were seen for many hours prior to hatch. After shell rupture the actual emergence required up to 6 hours.

As the temperature conditions approached the limits of egg hatch the mortality of the sample approached 100 percent. At the thresholds and upper limits many newly formed larvae died

between the time of shell rupture and full emergence. The data collected in this work are for fully emerged larvae only.

Under the above interpretation, egg development as indicated by eclosion is restricted considerably. At temperature extremes many embryos would appear to have completed development as indicated by the regular body movements and tracheal and mouthparts development, although some such eggs may not hatch at all. At temperatures 1 to 2 degrees beyond the developmental limits, these movements may also be detected, but the embryos are apparently too weak to break through the shell. Further,

variation in humidity on the development and hatching of fruit fly eggs. Such a study would be of more or less academic value since in reality fruit fly eggs are deposited and remain in environments saturated with moisture. Egg development in environments that are less than saturated has no practical value in a study of the bioclimatics of these insect species. It may be pointed out that laboratory rearing experience has indicated that when egg samples are allowed to dry out, that is, when humidity is allowed to approach that of the ambient air of the laboratory (55 percent daytime, 90 percent nighttime), egg mortality becomes extreme, even though temperatures are favorable.

#### STATISTICS OF EGG HATCH

Since the eggs in a sample hatch over a range of time, rather than all at once, the process of hatching or egg development must be considered statistically. This involves the matter of variation, the distribution of variation, and the reliability of the final statistic used to represent the entire sample. Some single-valued measure of time to complete development at different temperatures is required, and this value is best represented by a most probable statistic, *i.e.*, the average.

Previous workers investigating the effect of temperature upon insect growth and development have chosen different values, usually labeled with the term "average," for best representing their data. Where stated, most workers used the arithmetic mean of the variations in response of their samples (Bliss 1926; Peairs 1927; Koidsumi 1933, 1934; Melvin 1934; Shibata 1936a, 1936b; Edney 1945). Wardle (1930), working with *Lucilia sericata*, presented two values for the durations of stage with temperature, the mean maximum and the mean minimum times of response. To correlate duration of development with temperature he used the mean of these two values. Powsner (1935) stated that the hatching of eggs, the pupation of larvae, and the emergence of adults of *Drosophila melanogaster* are events distributed symmetrically in time and are therefore well represented by the arithmetic mean. However, he presented distributions of egg hatch at only two temperatures; 25° C., in which case hatching took place in a period of time according to a normal frequency curve, and 19° C., in which case, according to his data, hatching time was neither normally distributed nor symmetric about the arithmetic mean.

Huffaker (1944), in his work on *Anopheles quadrimaculatus*, used the average time for the first half of the egg sample to develop, and stated that this is a better statistic than the average time for all to develop, since the latter half of a sample was more likely to be affected by limited food supplies. This appears to be a

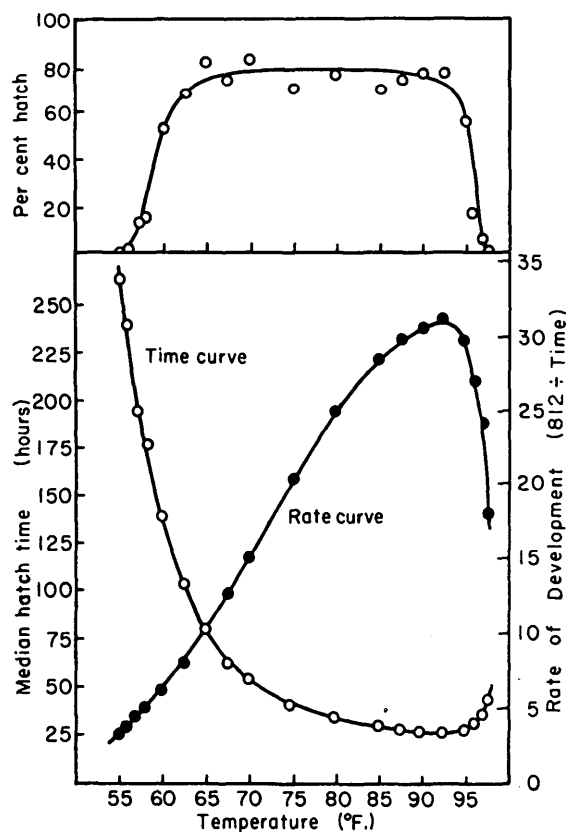


FIG. 1. Egg development of the oriental fruit fly, *Dacus dorsalis* Hendel: Relation between temperature and percent hatch (top curve), median time for development (time curve), and rate of development (rate curve).

at any given temperature it is not possible to determine for how long development has been completed prior to egg-shell rupture. This point would require other techniques for measuring growth, such as gains in weight, respiration, and so on.

However, in spite of the apparent indeterminacy of the end point of development when hatching is observed, this method has been used considerably in the past, it is reliable, and in the final analysis it is the most practicable.

No attempt was made to study the effect of

reasonable explanation of extreme variations in development (see below), although he provided no supporting data.

Larsen and Thomsen (1940), working with several species of flies including *Musca domestica*, used the minimum hatch period of the egg stage as the end point of development. They stated that as far as the egg stage is concerned it would probably have been preferable to use the mean hatch time, but they subscribed to the use of the minimum hatch time because of its simplicity and uniformity with their work on other stages. Shaw and Starr (1946), in a study of the effect of temperature on the development of *Anastrepha serpentina*, also used the shortest duration of development as measured by the first egg to respond.

variation in response is not symmetrically distributed in time (Williams 1937). Howe (1952) found that the cumulative curve relating molting of a sample of rice weevil larvae with time was skewed (see also Stanley 1946) and could be normalized by the conversion of time units to the logarithm of time. In this case it was the median of the length of stage that was measured, and Howe determined this statistic by means of probit analysis. In the hatching of *Anastrepha serpentina* eggs, when the cumulative hatch is plotted against the total developmental time, the resultant curve is an asymmetric sigmoid, which is straightened by the use of the probit transformation (Shaw and Starr 1946). In each case where probit analysis was used, hatching

TABLE II  
EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON EGG DEVELOPMENT OF THE  
MELON FLY, *Dacus cucurbitae* Coq.

TEMPERATURE (°F.)	EGGS INCUBATED (No.)	INCUBATION PERIOD (Hrs.)	HATCHING RANGE (Hrs.)	MEDIAN HATCHING TIME (Hrs.) <sup>a</sup>	PERCENT HATCH
52.0	618	....	..	.....	0
52.5	293	239.0	..	240.0	0.3
53.0	248	209.5	12	216.5	1.5
54.0	580	148.5	108	176.5±0.73	36.2
55.0	266	132.5	66	147.8±0.69	72.2
56.0	221	122.0	27	131.4±0.39	89.7
57.0	378	109.0	31	116.9±0.28	87.3
58.0	185	94.0	16	99.6±0.24	96.2
60.0	198	77.3	20	84.0±0.34	92.5
62.5	275	62.5	13	65.4±0.12	94.8
65.0	258	52.0	9	53.8±0.09	95.2
67.5	247	42.5	9	44.1±0.09	95.1
70.0	256	35.5	5	37.7±0.08	94.5
75.0	298	27.5	10	29.1±0.06	85.6
80.0	297	23.0	8	23.9±0.03	93.3
85.0	225	19.0	4	21.2±0.04	91.2
87.5	294	19.0	4	19.9±0.04	92.8
90.0	300	18.0	6	19.5±0.07	87.0
92.5	278	18.0	6	19.4±0.04	66.2
95.0	372	20.0	13	23.9±0.12	68.0
96.0	259	24.0	15	26.3±0.20	24.3
97.0	749	27.3	48	31.2±1.12	3.5
97.5	1418	40.0	24	43.5	0.02
98.0	1296	....	..	.....	0

They justified this statistic by reason of the relatively large proportion of eggs that hatched during the first part of the hatching period. However, these workers also reported that the incubation period, and therefore the time for the first egg that hatched, was not independent of the number of eggs that hatch. Rather, the larger the sample of eggs used, the shorter was the time for first hatch. The dependency of the hatching time upon sample size is not present when using means or medians.

Objections to the use of the arithmetic mean in this type of work are usually based upon the fact that it is abnormally affected by extremes in the range of response, especially when the

time was measured from the instant of first response—that is, duration of development less minimum incubation time.

The basic assumption in the use of probit analysis is the normal distribution of variation of individual growth periods as a function of time, taken directly from the toxicological theory of dosage-response as developed by Bliss (1935) and others. The propriety of this assumption can be ascertained easily by experimentation.

Treatment of hatching data in this manner, that is, by computing the median rather than the mean hatching time, eliminates the effect of extreme response and yet provides a statistic with the desired characteristic of minimum variability.

It is for this reason that medians were used in the present work rather than arithmetic means or minimum responses.

In the present study cumulative frequency hatching curves at several different temperatures were constructed in order to determine the manner of hatching of fruit fly eggs. For purposes of illustration, the hatch-time curve for eggs of the oriental fruit fly collected in the usual manner

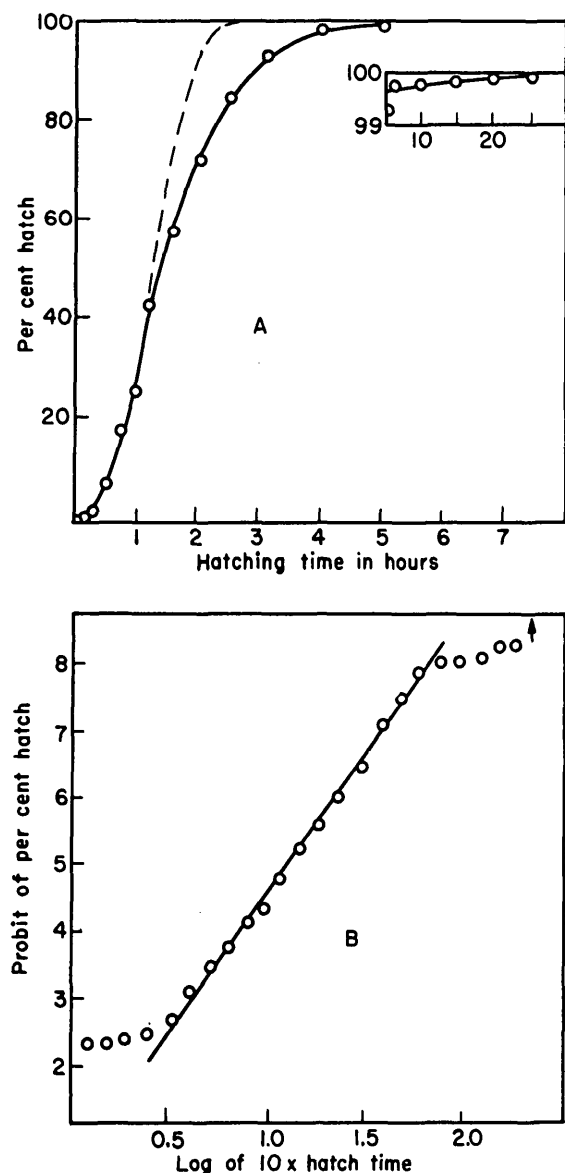


FIG. 2. Relation between percent hatch and hatching time for eggs of the oriental fruit fly, *Dacus dorsalis* Hendel, incubated at 80° F. A. Arithmetic scales. B. Log-probit scales.

and held at 80° F., is given in figure 2A. This response curve is skewed positive, as indicated by the considerable extension of the upper arm of the sigmoid curve. The added dashed line indi-

cates the shape such a curve should take, on the basis of distribution of the first half hatching, for the entire sample to be symmetrically distributed about the mean. Data from the same experiment are plotted in figure 2B according to the method of probits (Bliss 1937), using the log transformation to normalize. From this latter curve it can be seen that the log transformation has reduced the skewness of the cumulative frequency curve considerably, but the curve still retains some sigmoid character. According to Bliss, such a result derives from an undercorrection of the data by probits.

Other normalizing transformations, such as the log-log of time, reciprocal of time, reciprocal of the log of time, square root of time, and so on, fail to improve upon the shape of the probit curve. It may be deduced from this that the hatching of oriental fruit fly eggs at 80° is symmetrically distributed in relation to the logarithm of time, but not according to a normal curve. This being so, use of the median as a most probable statistic for egg hatch would appear to be more valid than use of the arithmetic mean, but determination of the median by the method of probits remains critical. If extreme percentiles of hatch are disregarded, say those giving probits below 3.0 and above 7.0, a good deal of the residual sigmoid character of the log-probit curve is eliminated. Under such circumstances the interpolation of the median becomes easier. This procedure was followed in the determination of the medians herein.

#### INFLUENCE OF TEMPERATURE ON FRUIT FLY EGGS

It is not proposed here to enter into a detailed discussion of the relation between temperature and insect development; this subject has been amply reviewed by others, including Crozier (1926), Shelford (1929, 1930), Belehradek (1930, 1935), Uvarov (1931), Janisch (1932), and Hoskins and Craig (1935). Therefore, only the following comments are made as a basis for describing the results of the present work.

The developmental-time data of Tables I to III, when converted to their reciprocals, are inadequately described by the simple rectilinear regression of developmental rate on temperature, as suggested by the early plant phenologists and advocated for insect growth by Sanderson (1910), Sanderson and Peairs (1913), Krogh (1914), and Blunck (1914), and since used by many other entomologists. Instead, the growth-rate data, plotted as in figure 1, describe temperature-velocity curves characterized by a sigmoidal increase from the threshold to a maximum point, followed by a post-maximum decrease to the upper developmental limit. This same pattern of development has been described empirically by Prochnow (1908; cited by Uvarov 1931) and later by Shelford (1927). In neither of these cases were mathematical relationships prescribed

for such curves, although Shelford assumed a straight-line relation between temperature and rate in the medial temperature range centered about what would be the inflection point of a sigmoid curve. Whether or not the rate data of figure 1 describe a straight line in the medial portion of the temperature range or better support a sigmoid curve is debatable. When the sigmoid is shallow at the inflection point, as in the present cases, the difference between a straight line and a curved one is minor.

Numerous mathematical expressions have been proposed for relating temperature and development, or developmental rates, such as the van't Hoff  $Q_{10}$  expression and the van't Hoff-Arrhenius modification thereof (van't Hoff 1884, and Arrhenius 1915), the thermal constant relation of Sanderson and Peairs (1913), and the

point of fastest growth, or asymmetric where these actions are of unequal intensity.

Larsen and Thomsen (1940) and Huffaker (1944) provide examples of the application of symmetric catenary curves, while Cook (1927) uses an asymmetric catenary curve to describe the growth of cutworms. However, in most such experiments there are only one or two temperatures above the point of fastest growth that define this portion of the developmental curve. This renders it difficult to determine whether this part of the curve is actually symmetric with the remainder or not.

Pradhan's (1946) formula is based upon the assumption that growth is accelerated exponentially with temperature, but that the amount of acceleration decreases uniformly from the lower threshold to the upper developmental limit. The

TABLE III  
EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON EGG DEVELOPMENT OF THE  
MEDITERRANEAN FRUIT FLY, *Ceratitis capitata* (WIED.)

TEMPERATURE (°F.)	EGGS INCUBATED (No.)	INCUBATION PERIOD (Hrs.)	HATCHING RANGE (Hrs.)	MEDIAN HATCHING TIME (Hrs.) <sup>a</sup>	PERCENT HATCH
52.5	663	.....	..	.....	0
53.0	270	509.0	10	516.0	1.1
54.0	853	373.0	130	423.0±1.50	25.4
55.0	615	316.5	112	363.0±1.46	44.1
56.0	666	303.5	31	309.7±0.40	65.5
57.0	305	238.0	38	251.3±0.46	88.5
58.0	332	235.0	12	237.8±0.13	89.8
60.0	250	171.3	32	185.3±0.42	95.2
62.5	270	138.5	15	142.7±0.23	94.1
65.0	223	106.0	25	112.9±0.22	88.3
67.5	308	88.0	17	92.9±0.12	97.1
70.0	210	73.5	11	76.7±0.13	87.1
75.0	456	56.5	10	57.6±0.06	95.2
80.0	478	44.3	10	44.8±0.03	89.7
85.0	207	36.8	6	38.4±0.08	82.6
87.5	300	35.0	6	36.2±0.06	86.0
90.0	310	34.0	5	34.7±0.06	96.0
92.5	558	35.3	8	37.4±0.04	94.8
95.0	613	38.0	14	43.6±0.25	24.3
96.0	1141	45.0	14	47.2±0.90	0.4
96.5	552	.....	..	.....	0

exponential functions of Janisch (1925), Belehradsek (1926), Davidson (1944), and Pradhan (1946). All these relations were tested against the data presented here, but only the formulas of Janisch and Pradhan include the required sigmoidal characteristics.

Janisch's (1925) expression, mathematically a catenary curve when relating temperature and developmental time, is derived from two exponential functions presumed to describe, respectively, the accelerative action of increases in temperature upon growth and the decelerative action of high temperatures above the point of fastest growth. The resultant catenary may be symmetric when the accelerative and decelerative actions are of equal intensity on each side of the

resultant expression for relating growth rates and temperature takes the form of a bell-shaped curve. The premise that the accelerative action of increases in temperature decreases *uniformly* results in a temperature-velocity curve symmetric about the point of fastest growth. Pradhan does not provide sufficient data in the high temperature range to permit the accurate evaluation of this point.

Observation of the plotted data for fruit fly egg development shows that the accelerative effect of increasing temperatures upon growth and the decelerative effect of high temperatures are not quantitatively equal; hence, an asymmetric curve is required here. This seems to exclude Pradhan's expression as now developed. How-

ever, an asymmetric catenary may be fitted to the data of figure 1 only by considering the descending and ascending portions of the time temperature curves individually and adjusting the origins and intercepts of the two exponential functions derived from each. While a formula may thus be derived to fit the data rather closely throughout the medial and high temperature ranges, the low temperature range is less adequately described. Further, the resultant catenary is of greater complexity than Janisch's (1925) original formula.

For *Dacus dorsalis* a catenary that fits the data well is

$$y = 24.2 + 1.18(1.1425^t + 2.385^{-t})$$

where  $y$  is the developmental time and  $t$  is the difference between the temperature of the origin of the two empirical curves  $94.4^\circ$  and the test temperature, the latter determined graphically by plotting developmental times on a logarithmic scale against temperature on an arithmetic scale. By adjusting the origin of the log scale, that is, by subtracting a constant from the set of developmental times, the two limbs of the plotted curve tend towards straight lines. For *Dacus dorsalis* this constant was found by trial to be 24.2 hours, the slope of the straight line determined by the low temperature limb being 1.145, and that determined by the high temperature limb being 2.385. The two straight lines intersect at the point  $94.4$  degrees and  $1.180$  hours; the expressions describing each of these lines are therefore  $1.180(1.145)^{94.4-t}$  and  $1.180(2.385)^{-94.4+t}$  where  $t$  is the actual temperature. The overall expression given above is the sum of these two factors, where  $t = 94.4 - t'$ , and the constant 24.2 is restored. The minimum point of the catenary falls at  $92.5^\circ$ , coinciding with the experimental temperature at which fastest growth occurs.

In figure 1, rates of egg development have been plotted in terms of developmental units, according to the method of Shelford (1927, 1929). This procedure depicts growth rates in terms of absolute units (fractions of the total development per hour, referred to as developmental units) rather than of relative units (reciprocals of developmental time; percentages of growth per hour), and permits direct comparison of different species requiring different amounts of heat at different intensities for completion of growth. Comparisons of growth rates at different temperatures, using relative units are possible for a given species; but such units provide no measure for comparison of species, since the total growths finally attained by each species are given the same numerical values (unity, 100 percent, etc.). The solid lines in the figure are curves fitted by eye and bear no mathematical relation to the variables under consideration. The catenary for *Dacus dorsalis*, whose formula is given above, follows rather closely the time curve of figure 1

from the upper developmental limit down to  $60^\circ$ . At temperatures below this value the catenary diverges from the time curve, rising less steeply until at the threshold,  $55^\circ$ , it indicates a developmental time of 248 hours.

The lowest temperatures at which the egg stage of the three species of fruit flies could complete development, as indicated by hatching are as follows: *Dacus cucurbitae*,  $52.5^\circ$ ; *Ceratitis capitata*,  $53.0^\circ$ ; and *D. dorsalis*,  $55.0^\circ$ . At these temperatures the percentage recovery approached zero. No eggs hatched, even when large numbers were used, at a constant temperature one-half degree below these values. Therefore, it is considered that the thresholds of development of the egg stage of these species lie between these narrow limits.

The rate of development of the eggs, as measured by developmental units, does not vary in direct proportion with temperature except possibly in a range of temperatures between the approximate limits  $60^\circ$ – $85^\circ$ . These are called medial temperatures in accordance with the terminology of Shelford (1927). With increasing temperatures from the thresholds up to  $60^\circ$  the developmental rates increase with temperature in greater than direct proportion, and values for these rates lie above the line followed by the data in the medial range. This result indicates that the determination of the threshold of development by extrapolation of the linear portion of the rate-temperature curve may not be experimentally accurate. (See also Peairs 1927; Hoskins and Craig 1935).

If the medial portions of the rate curves are projected so as to intersect the rate axis, the temperature values so determined (corresponding to the alpha points of Krogh (1914)) are as follows: *Dacus cucurbitae*,  $52.5^\circ$ ; *Ceratitis capitata*,  $55.0^\circ$ ; and *D. dorsalis*,  $55.0^\circ$ . These values rather closely correspond to the experimentally determined thresholds of development. However, it would seem quite important to insure that only the medial portion of the rate-temperature curve be used for this extrapolation. Using the method of Krogh (1914) as applied by Bodenheimer (1925, 1951), wherein a straight line is fitted to the entire set of data of the ascending arm of the rate-temperature curve, the present data would yield intercepts as follows: *Dacus cucurbitae*,  $50.0^\circ$ ; *Ceratitis capitata*,  $52.0^\circ$ ; and *D. dorsalis*,  $52.5^\circ$ . These are all lower than both the experimentally determined thresholds and the alpha values given above, owing to the fact that the sigmoid nature of this part of the rate curve yields straight lines of shallower slope than do the medial zones.

Above the upper medial limits (about  $80^\circ$ ) the rates of development begin to diverge from the linear relationship, passing through maximum values between  $90^\circ$  and  $92^\circ$  and eventually decreasing as the upper limit is approached.



This decrease in rate with high temperatures is accompanied by a decrease in recovery, until at the upper limit the percentages hatching are zero. The upper limits of development for the three species of fruit flies have been determined experimentally as follows: *Ceratitis capitata*, 96.0°; and *Dacus dorsalis* and *D. cucurbitae*, 97.5°. At constant temperatures one-half degree higher than these values, eggs of the respective species do not hatch.

The maximum rates of development of the eggs of these insects occur over a more or less narrow zone of temperatures, between 90° and 92.5°. Such rates are accompanied by recoveries as high as occur at any other temperatures. Hence, such rates may be termed optimal velocities for growth, and the corresponding temperatures may be considered the optimal temperatures for growth. Uvarov (1931) defines the optimum temperature for development as that point at which the greatest number of individuals develop in the shortest time. He states that such an optimum is not necessarily the temperature at which the swiftest growth occurs, because this point, lying as close as it does to the upper temperature limit, is usually accompanied by poor

characteristics of the egg stage of the insects concerned. From these data it would appear that the two aspects of development, rate and tolerance to extremes, do not necessarily vary in the same way among different species. Relative rates are indicated by the thermal constants (degrees above the alpha point multiplied by the hours required to hatch, see Sanderson 1910; this is also the developmental total of Shelford 1927), which in the present cases are computed from the medial portions of the rate-temperature curves. *Dacus cucurbitae* eggs show the lowest thermal constant, the highest optimal temperature, and the widest tolerance to low and high temperatures. *D. dorsalis* eggs, while showing an intermediate thermal constant and hence intermediate growth rates, are somewhat less tolerant to cool temperatures. *Ceratitis capitata* eggs show the highest thermal constant and hence the slowest growth rates, and are almost as tolerant to cool temperatures as *D. cucurbitae* eggs, but are not so tolerant to high temperatures. The optimum temperature for this species (90°) is also lower than those for the other two species.

At any medial temperature the viability of *Dacus cucurbitae* and *Ceratitis capitata* eggs is

TABLE IV  
THERMAL CHARACTERISTICS OF EGG STAGE OF THE THREE SPECIES OF FRUIT FLIES  
*Dacus dorsalis*, *D. cucurbitae*, and *Ceratitis capitata*

SPECIES	TEMPERATURE (°F.)			THERMAL CONSTANT (HR.-DEGREES)
	THRESHOLD LIMIT	OPTIMUM	UPPER LIMIT	
<i>D. dorsalis</i>	55.0	92.5	97.5	812
<i>D. cucurbitae</i>	52.5	92.5	97.5	660
<i>C. capitata</i>	53.0	90.0	96.0	1144

survival. In the present cases, however, it appears that the optimal temperature as defined by Uvarov and the temperature of maximum rate coincide.

These optimal temperatures are slightly higher than those found by Shibata (1936a, 1936b) who reports the maximum rates for eggs of *Dacus dorsalis* and *D. cucurbitae* to be 89.5°.

The range of time over which hatching takes place depends upon the temperature. In the medial range of temperatures the hatching range is relatively short, ranging from 3 to 9 hours for *Dacus cucurbitae*, 4 to 17 hours for *D. dorsalis*, and 5 to 25 hours for *Ceratitis capitata*. At extremes of temperature, however, this hatching range becomes extended considerably, ranging from 3 to 4 days for the first two species, and up to 5 days for the last species. At these temperature extremes the range of hatching is also dependent upon the number of eggs used in the sample, since at these conditions egg mortality is high.

In Table IV are summarized the various thermal

higher than that of *D. dorsalis*. In general, the effects of temperature upon percentage hatch are the same for all three species: low hatch at temperature extremes and maximum hatch throughout the medial range.

It is possible that the form taken by the curves relating percentage of hatch and temperature may offer a means of checking the position of the temperature limits for development on the biokinetic scale. In the cases of eggs of *Dacus cucurbitae* and *Ceratitis capitata* the rising and descending portions of these inverted U-shaped curves are quite steep. Extrapolation of these curves to the zero-percent axis should yield intercepts at the temperatures corresponding to the biokinetic limits. In the case of *D. dorsalis* eggs (figure 1) these portions of the curve are somewhat sigmoidal, with slightly shallower slopes in the vicinity of zero-percent hatch, indicating that extrapolations here require experimental verification. In any event, unless these portions of the recovery-temperature curves become asymptotic with the abscissa, the nature

of these curves adds verification that the actual temperature limits discussed above have been closely approximated experimentally.

Comparison of the present work with that of Shibata (1936a) on *Dacus dorsalis* indicates that eggs from Formosan-bred fruit flies hatch over a wider range of temperatures than do those from Hawaiian-bred flies. The experimentally determined limits for eggs of this species in Formosa fell below 53.6° and above 100.5°, a biokinetic spread over four degrees wider than that obtained in Hawaii. On the other hand, the temperature ranges over which *D. cucurbitae* eggs were noted to hatch were in closer agreement between the Formosan and Hawaiian stocks of flies. Shibata (1936b) obtained first hatch at 53.6° and none at 51.8°, while eggs in Hawaii hatched at 52.5° and not at 52.0°. At the upper limit, Shibata observed hatch at 95° and none at 97°, while the data herein show hatch at 97.5°, but none at 98.0°.

The data presented herein may also be utilized in the experimental breeding of fruit fly stocks for other than bioclimatic considerations. By use of the correlations between developmental periods and temperatures, fruit fly eggs may be incubated under conditions that will permit hatching to occur at predetermined times or after predetermined delays. Such a situation is sometimes desired in the selection of strains of insects resistant to insecticides or tolerant to temperature extremes or other environmental stresses, and where the selecting procedure results in but a few survivors for testing and for breeding stocks of the following generation. Both the need for large stocks of adults (or other stages) of uniform age for further selection, and the need in standard mass-rearing techniques for large numbers of larvae, require that as many eggs as possible be gathered from the few gravid females available. This can be done usually only by gathering successive batches of eggs over several days time and incubating the successive batches under different temperatures so that all will hatch at the same time. In the case of *Dacus dorsalis* for example, if eggs gathered one day are incubated at 66°, eggs of the second day at 73°, and eggs of the third day at 90°, the three batches will hatch in 72, 48, and 25 hours, respectively, or all at about the same time on the fourth day. This procedure yields three times as many individuals of a uniform age as would otherwise be possible.

In a similar vein, in the mass rearing of fruit flies it is inconvenient to have large numbers of eggs hatching during the night or off-work hours, since for best results the artificial larval medium should be made up fresh and inoculated with eggs just at the time of hatching. If the larval medium is made up some time prior to hatching, deleterious molds and bacteria form on it; and if newly hatched larvae are held for some time before they are placed on the medium, mortality

is high. By using the time-temperature data and incubating the eggs at the proper temperatures this problem can easily be avoided.

#### SUMMARY

Eggs of the oriental fruit fly, *Dacus dorsalis* Hendel, the melon fly, *D. cucurbitae* Coq., and the Mediterranean fruit fly, *Ceratitis capitata* (Wied.), were incubated in constant temperature water baths and the time required to complete embryonic development, as measured by hatching, was observed. At any given temperature there are individual variations in rate of growth among eggs, and hatching proceeds according to a skewed distribution that can be normalized by a logarithmic transformation. Because of this, developmental periods were computed from the medians rather than from the arithmetic mean of the hatching periods. The variations in growth rate are greater at high and low temperatures than at medial temperatures.

The relation between growth rate and temperature is sigmoidal rather than rectilinear, with an actual decrease in rate at high temperatures. The shape of the growth-rate curve approximates the empirical Shelford curve, and may be rather closely approximated by an asymmetric catenary function. Egg viability at different temperatures follows an inverted U-shaped curve with minimum hatch at the temperature extremes, approaching zero at the thresholds and upper developmental limits, and with maximum hatch in the medial temperature range.

Melon fly eggs developed at the lowest temperatures, in the fastest time, and over the greatest range of temperatures. Mediterranean fruit fly eggs developed over a slightly narrower temperature range, but at slower rates. Oriental fruit fly eggs were affected most by low temperatures, having the highest temperature threshold, and developed at intermediate rates. Optimum development for all three species occurred between 90° and 92.5°. Threshold values were as follows: melon fly, 52.5°; Mediterranean fruit fly, 53.0°; and oriental fruit fly 55.0°. Upper temperature limits for the same species were 97.5°, 96.0°, and 97.5°, respectively.

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