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PROPAGATION OF THE ORIENTAL FRUIT MOTH UNDER CENTRAL CALIFORNIA CONDITIONS

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PROPAGATION OF THE ORIENTAL FRUIT MOTH UNDER CENTRAL CALIFORNIA CONDITIONS[1]

LESLIE M. SMITH[2] and FRANCIS M. SUMMERS[3]

INTRODUCTION

SINCE 1943 the State Department of Agriculture has discovered low populations of the Oriental fruit moth, *Grapholitha molesta* Busck, in several widely scattered peach-growing localities in central California. The San Joaquin and Sacramento valleys which comprise this area contain a large proportion of all peach plantings within the state. These valleys have a different climate from that encountered by the Oriental fruit moth in other important peach-producing states. The very hot, dry summers and mild, foggy winters, the extensive practice of irrigation, and the very long growing season—averaging 289 days in the vicinity of Fresno (Bonnett, 1941)[4]—are environmental factors which may affect the future development of the Oriental fruit moth populations.

In the course of a general study of the life history of the Oriental fruit moth in central California, a number of experiments were performed in the insectary at Dinuba to determine whether or not the hot summer climate of the central-valley area retards its propagation; and, if so, whether it is retarded enough to reduce the potentiality of the moth as a pest. It is the purpose of this report to describe this phase of the life-history work, and to present other observations on mating and oviposition which have a bearing on the dispersal and build-up in thinly distributed populations of Oriental fruit moths such as now occur in this part of the state.

METHODS AND STOCKS

The moths were reared in a screened insectary and subjected as nearly as possible to outdoor conditions. The cages and other receptacles were constructed of light materials, thin sheet plastic and cheesecloth or gauze, in order to minimize the time required for their interiors to come into equilibrium with atmospheric conditions during rapid weather changes.

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[4] See "Literature Cited" for citations, referred to in text by author and date.

When Oriental fruit moths from several localities were compared in side-by-side laying tests, it became apparent that all were not equally prolific. They were then given stock designations according to the locality from which the larvae were taken. The original insectary moths were reared from larvae obtained from a peach orchard in Tulare County; they were designated as the Dinuba stock. The moths herein designated as the southern California stock were obtained later from orchards in Orange County. Two other stocks were developed from larvae taken in Fresno County, in central California. They are subsequently referred to as the Parlier I and Parlier II stocks. The Parlier I stock was started from a pair of moths, Parlier ♀ × Dinuba ♂.

MATING HABITS

Oriental fruit moths usually emerged from their cocoons in the morning on sunny days, between 7 a.m. and 11 a.m. Individuals of both sexes were sometimes capable of mating on the day of emergence, though ordinarily the first successful matings were not made until the second or third day of adult life. Casual observations of copulating pairs indicate that mating occurs in the evening, after 5 p.m., which coincides with the period of greatest flight activity and oviposition by older individuals. During the cool spring months, copulating pairs were sometimes seen in the early afternoon.

The number of successful matings which males are capable of making in one overnight period was experimentally determined for six males. Each of six 2-day-old unmated males was placed in a small cage with five 2-day-old females (1st to 5th in table 1) and allowed to remain in the cage overnight. On the following morning the males were discarded and the thirty females from the six cages were placed each in a separate cage and left for 10 days. At the end of this period the number of eggs laid by each female and the number which later hatched were recorded. The numbers of eggs deposited are given by the upper figures, and the numbers hatched by the lower figures in each cell of table 1.

Of the six males tested, three (nos. 3, 5, and 6) apparently mated with but one female each. The latter deposited average broods of viable eggs. The other three males (nos. 1, 2, and 4) apparently attempted to mate with more than one female but only one female from each cage produced a normal brood. The unsuccessfully mated females laid nonviable eggs. The numbers of these eggs were, with one exception, greater than expected from unmated females. Unmated females occasionally laid one or two eggs during their lives but none of the eggs were ever observed to hatch. The average brood expected for mated females of the stock used is approximately 114 eggs, over 85 per cent of which are viable when deposited on wax paper.

Females mated sucessfully during a brief association (12 hours) with males appeared to lay as many eggs as those kept with males throughout the laying period.

Males may retain their fecundity throughout life. This was demonstrated by an experiment in which the same males were mated, on successive days, to different young females (table 2). The results are shown as the number of eggs laid in ten days (upper figure) by each of the test females, and the number of eggs which later hatched (lower figure).

Five of the males (A to E) were placed with the first females on the day of emergence and with different females on each of the five succeeding days. All of the test females were less than 12 hours of age when presented to the males. Successful matings did not occur until the males were at least 3 days of age (males B and C). One male (A) was unable to make a fertile union with any of the six females presented on different days, possibly for the reason

TABLE 1

RESULTS OF TESTS TO DETERMINE THE NUMBER OF SUCCESSFUL MATINGS MADE BY MALES DURING ONE 12-HOUR (OVERNIGHT) PERIOD

Designation of males	Oviposition record for each of the 30 test females: Number of eggs laid / *Number of eggs hatched*				
	1st	2nd	3rd	4th	5th
1	0	102/*89*	0	10/*0*	18/*0*
2	147/*143*	4/*0*	0	5/*0*	0
3	139/*129*	0	0	0	0
4	1/*0*	3/*0*	0	0	120/*115*
5	0	0	0	0	141/*132*
6	0	0	0	167/*163*	0

that the females were not ready for mating during their first 12 hours as adults.

The procedure was slightly modified for a second group of five males (F to J). They were presented to the first of the females on the day after emergence; and all of the test females were 24 hours old when placed with them. Two of the males (G and H) mated on the second day, and all mated on the third day. This series was discontinued after 5 days.

For a third group of five males (K to O), the mating trials with females 24 hours old were started on the day after emergence and continued for 15 days, or until the first male died. Males K to O mated irregularly, although the number of failures occurred with greater frequency after the first 8 days of life. Forty-two of the seventy-five females with which they were tested laid fertile eggs, and twelve were induced to lay more than two infertile eggs. The data of the long series suggest that there may be a decline of mating capacity in males of advanced age.

A limited number of tests were made to find out whether or not moths of both sexes are able to mate for the first time in later life. Young females, 24 hours of age, were found to be capable of laying viable eggs when mated to previously unmated males 3 to 10 days of age; and, in reciprocal tests, pre-

TABLE 2

THE NUMBERS OF EGGS DEPOSITED IN TEN DAYS BY YOUNG FEMALES WHEN MATED TO MALES OF DIFFERENT AGES

Age of males in days	Males first mated on day of emergence					Males first mated on day after emergence									
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
	Oviposition records for each of the test females: Number of eggs laid / *Number of eggs hatched*														
1	4/*0*	0	0	0	4/*0*	...	...	...	...	...	...	...	...	...	...
2	25/*0*	7/*0*	0	1/*0*	4/*0*	0	15/*11*	100/*92*	1/*0*	1/*0*	116/*110*	148/*139*	112/*106*	128/*127*	2/*0*
3	0	112/*108*	101/*96*	0	0	171/*161*	146/*110*	150/*147*	141/*136*	140/*136*	0	186/*177*	0	0	7/*0*
4	29/*0*	0	133/*126*	18/*0*	140/*120*	0	55/*49*	94/*90*	88/*87*	4/*1*	126/*100*	153/*148*	0	158/*149*	171/*159*
5	7/*0*	112/*111*	218/*198*	146/*129*	191/*164*	2/*0*	87/*83*	134/*126*	127/*125*	118/*116*	9/*0*	187/*166*	188/*186*	163/*158*	119/*103*
6	0	177/*158*	0	119/*101*	3/*0*	...	132/*124*	0	206/*198*	187/*185*	0	182/*166*	145/*118*	115/*99*	112/*92*
7	...	...	...	...	...	...	...	...	...	...	78/*70*	27/*26*	94/*92*	167/*157*	0
8	...	...	...	...	...	...	...	...	...	...	7/*0*	104/*102*	89/*82*	65/*64*	53/*46*
9	...	...	...	...	...	...	...	...	...	...	18/*16*	3/*0*	101/*83*	92/*91*	12/*10*
10	...	...	...	...	...	...	...	...	...	...	39/*36*	3/*0*	3/*0*	13/*4*	0
11	...	...	...	...	...	...	...	...	...	...	0	7/*0*	0	0	2/*0*
12	...	...	...	...	...	...	...	...	...	...	0	199/*198*	175/*168*	141/*137*	126/*124*
13	...	...	...	...	...	...	...	...	...	...	0	18/*12*	0	2/*0*	40/*15*
14	...	...	...	...	...	...	...	...	...	...	1/*0*	64/*55*	0	28/*13*	0
15	...	...	...	...	...	...	...	...	...	...	7/*0*	25/*0*	151/*125*	166/*157*	2/*0*
16	...	...	...	...	...	...	...	...	...	...	7/*0*	115/*86*	0	3/*0*	25/*0*

viously unmated females 3 to 10 days of age mated successfully with males 24 hours of age. Previously unmated males and females, up to 10 days of age, produced broods of viable eggs when mated together. Quantitative data are not available at the present time for matings of this type.

OVIPOSITION

General Laying Habits. Oviposition was observed to begin on the second day after emergence, or later, according to conditions of sunlight and temperature. Mating often occurred on the evening of the day of emergence in midsummer, and the first eggs frequently appeared 24 hours later. Females were not observed to lay on the day of the initial mating. The duration of the true preovipositional period was more commonly 3 to 5 days, with periods ranging up to 14 days in the cool weather of early spring.

On warm, sunny days the peak of oviposition occurred between the time of sunset and full darkness. Very few eggs were laid in the early morning hours and none were ever observed to be laid during the day. These observations on the time of laying at Dinuba agree generally with those made by Stearns and Neiswander (1930) on the Oriental fruit moth at Wooster, Ohio. They noted that, in July, oviposition usually started between 4 and 5 p.m. and continued until about midnight, and that approximately 90 per cent of the eggs were deposited between 6 and 9 p.m.

The temperature range within which oviposition is possible could not be determined precisely by the methods used in this work. According to tests performed at Dinuba during 1946, there was no obvious decline in oviposition at the peak summer temperatures recorded in the insectary (table 5, page 376). The highest maximum temperature recorded during oviposition tests was 104° F. The lowest 1946 temperatures recorded during the tests occurred on October 4, 5, and 6, during which time 100 females of the southern California stock averaged 25.6 eggs a day each. The insectary temperatures for the three days averaged 68.3° at sunset (approximately 5:37 p.m.) and 61.7° at 7:00 p.m. Others have noted that oviposition declines when the temperature falls below 70° at sunset (McConnell, 1934) and that practically no eggs are laid when the temperature during the normal egg-deposition period is below 60° (Peterson and Haeussler, 1930). A minimum temperature of 55° is given by Cagle (1930).

The ovipositional period averaged 10.1 days during 1945, with 19 days as the longest noted for any of the insectary strains. The maximum number of eggs generally appeared on one of the first 3 days of the laying period. The largest number of eggs deposited by a single female on the first laying day was 45, which was also the maximum observed for any day during oviposition. After beginning abruptly, the trend of oviposition varied considerably during relatively uniform weather conditions. Some females continued to oviposit at a reduced rate after the peak, producing 8 to 15 eggs daily until near the end of the laying period. Others oviposited heavily during the first half of the laying period but continued thereafter with only a small number of eggs each day. Many laid haphazardly throughout, and a few moths of the Dinuba stock did not lay at all.

During periods of low temperatures, the reproductive life of females was prolonged and the eggs were distributed more evenly throughout the laying period.

The most prolific of the stocks laid an average of 114.1 eggs per female during 1946, and the maximum number laid by any female under observation was 234.

A composite daily production record for 119 females, each one placed in a small cage with three males, is given in table 3 to show how oviposition

TABLE 3
OVIPOSITION IN RELATION TO AGE OF FEMALES
DINUBA STOCK, 1945

	Spring generation	First generation	Second generation	Third generation	Total or average
Ovipositing period	Apr. 22–May 31	June 13–July 23	July 15–Aug. 22	Aug. 13–Oct. 3	....
Number of females	19	36	33	31	119
Total eggs laid	913	1,597	1,313	1,605	5,428
Age of females, days	Cumulative per cent of eggs laid				
2	1.0	1.5	8.2	1.3	3.0
3	6.4	11.8	12.6	11.1	10.9
4	22.8	22.3	20.3	21.5	21.8
5	43.8	31.6	27.1	33.0	33.0
6	58.3	44.0	42.7	38.4	44.5
7	73.0	53.1	51.8	46.5	54.3
8	79.8	61.4	64.6	59.5	64.7
9	87.3	71.1	71.8	66.9	72.8
10	90.7	77.2	80.3	76.7	80.0
11	92.9	84.5	87.5	81.4	83.9
12	96.0	88.5	92.7	86.3	90.0
13	97.3	92.5	96.6	92.0	94.1
14	98.2	96.6	98.6	94.5	96.7
15	98.7	98.2	99.5	96.9	98.2
16	98.8	99.0	99.5	97.6	98.8
17	99.2	99.3	99.9	99.4	99.5
18	99.9	99.8	100.0	99.9	99.8
19	100.0	100.0	....	99.9	99.9
20	....	....	....	100.0	100.0

varied according to age of the females. The build-up in numbers of eggs deposited by the moths as a group was not so rapid as for individuals because of variations in the length of the preovipositional periods of the females comprising the group. Four generations of females are shown to have laid approximately two thirds of their eggs during the first 8 days of adult life. Later work indicates that the total number of eggs deposited by this group of females was below average—probably because of the type of food on which the larvae were reared—but that the trend of laying was normal.

Variations in the number of eggs laid by individual females are shown by the frequency distributions in table 4.

Oviposition under Different Weather Conditions. In order to compare numbers of eggs deposited per female under different weather conditions, ovipositional tests were made at intervals between April 18 and September 9, 1946.

Freshly emerged females were counted into one or more cages and provided with an excessive number of males, in the approximate ratio of 65 males to 50 females. Possible crowding effects were minimized by placing not more than 50 females, or 115 moths of both sexes, in one cage. When the number of females available was not an even multiple of 50, they were equally distributed in two or more cages. The cages used for this purpose were thin-walled plastic tubes, 4½ inches in diameter and 6 inches long, each covered on one end with surgical gauze and on the other end with bleached muslin. The use of the muslin on the end placed nearer to the light source reduced flight

TABLE 4

VARIATION IN THE NUMBERS OF EGGS LAID BY FEMALES OF TWO STOCKS, 1946

Strain	Number of females observ'd	Number of eggs laid												
		0	1–20	21–40	41–60	61–80	81–100	101–120	121–140	141–160	161–180	181–200	201–220	221–240
		Per cent of females observed												
Dinuba....	133	12.8	14.3	7.5	11.3	13.5	15.8	10.5	9.8	2.2	1.5	...	0.8	...
Southern California	132	....	5.3	2.3	11.4	12.9	10.6	14.4	12.1	8.3	12.1	5.3	3.8	1.5

injuries to a very low level. In fact, after the techniques of transferring moths from cage to cage were perfected, the number lost by accident proved to be negligible. A lidlike arrangement at one end of the cage facilitated the changing of the wax-paper lining on which the eggs were deposited. A compressed pad of wet cotton in a Syracuse dish served as the drinking fountain and humidifier. The cages filled with moths were suspended on wood frames adjacent to the south screen wall of the insectary, where they received diffuse sunlight during the early morning and late afternoon.

Earlier experience with Oriental fruit moth oviposition showed that the variations in numbers of eggs laid by small, homologous samples of concurrently laying moths were apt to be greater for short periods of time than for long periods of time. Consequently, a 7-day time unit was adopted as a compromise between highly variable production under uniform weather conditions during 1- or 2-day test periods, and more uniform production but highly variable weather conditions during long, overlapping test periods. However, for estimating total laying capacity, seven of the twenty-one tests were run to completion—that is, for the entire laying period.

The average number of eggs produced per female in 7 days and the average temperatures during the test periods are given in table 5. The data show that oviposition did not diminish to any great extent during periods of highest average temperatures. In fact, for the southern California and Dinuba stocks, the highest averages were obtained during periods having the highest average temperatures. The averages obtained for small samples of Parlier I moths do not show a well-defined trend. Except for low averages in June, these moths oviposited about as well in hot weather as in cool weather. In five out of six tests made during July and August with Parlier I moths, the averages were well above the weighted mean for the series of tests.

All of the moths used in the tests were derived from larvae fed on green peaches, the quality of which varied according to the size of the fruit. The moths used in the tests during April are shown to have deposited more eggs than those tested in June (table 5). These were spring-generation moths derived from larvae fed on large green peaches (Miller's Late variety) during

TABLE 5

AVERAGE NUMBER OF EGGS DEPOSITED PER FEMALE DURING THE FIRST SEVEN DAYS OF THE OVIPOSITIONAL PERIOD

Initial laying date (1946)	Average temperatures for 7-day periods		Stocks tested					
			Southern California		Dinuba		Parlier I	
	Daily mean	At 7:00 p.m.	Number of females	Average number eggs per female	Number of females	Average number eggs per female	Number of females	Average number eggs per female
Apr. 18	66.6	75.4	54	41.1	60	42.0	10	57.8
Apr. 20	68.3	76.4	74	59.2	125	50.1	35	68.7
Apr. 24	67.9	75.9	40	57.7	150	40.8	23	54.5
June 6	68.3	78.6	110	37.7	72	17.4	90	21.7
June 8	69.9	79.7	96	38.0	97	27.0	83	29.0
June 11	71.6	82.0	111	65.2	120	33.7	50	25.8
June 22	72.8	81.7	..	....	110	28.3	..	....
June 25	75.9	84.7	..	....	100	43.2	..	....
June 27	77.3	85.9	..	....	100	48.2	..	....
June 29	78.8	88.3	..	....	150	32.3	..	....
July 10	79.7	89.7	250	102.8	111	56.7	100	57.9
July 12	79.1	89.3	150	92.6	80	37.8	100	60.1
July 15	81.6	90.1	150	101.9	75	56.2	89	52.2
July 26	79.5	88.7	..	....	135	69.9	..	....
July 30	81.4	90.7	135	97.2	..	....	..	....
Aug. 6	80.8	90.3	150	106.0	75	59.8	90	38.1
Aug. 8	81.3	90.1	120	88.6	200	38.7	50	52.6
Aug. 10	80.1	88.3	150	82.9	200	33.7	100	49.1
Aug. 23	76.6	83.9	100	91.4	200	44.7	..	....
Aug. 25	74.5	81.1	77	96.4	200	49.6	..	....
Sept. 27	70.6	72.4	100	81.5	..	....	..	....
Total or weighted mean	....	....	1,867	83.4	2,360	42.7	820	45.5

the fall of 1945. The low average made by first-generation moths in June was probably due to the fact that very small, prethinning peaches were fed to the first batches of 1946 larvae. Because the small peaches tended to dry out, the larvae were obliged to transfer to new ones added from time to time. Therefore the increase in production, beginning in late June and continuing through July, may be attributed to rising temperatures, to the increasing size of the peaches provided as food for the larvae, or to both factors.

Oviposition by Moths of Different Stocks. Averages of the numbers of eggs deposited per female during complete ovipositional periods are listed in table 6. The weighted means of 114.1 eggs per female for moths of the southern California stock and 56.5 eggs per female for those of the Dinuba stock are assumed to differ significantly, since the ratio between them is approximately 2:1. On the other hand, the difference between the mean number of eggs produced by Dinuba and Parlier I moths is possibly not significant, especially in view of the small differences obtained in the 7-day tests.

Another stock, Parlier II, was introduced into the insectary during 1946. In one test made near the end of the season, 74 Parlier II females laid an average of 81.7 eggs as compared with an average of 143.0 eggs per female for southern California females laying on the same dates (table 6). The ratio of the averages for Parlier II and southern Californa moths in this one test (81.7/143 = 0.57) agrees closely with the ratio between the means obtained

TABLE 6

AVERAGE NUMBER OF EGGS DEPOSITED PER FEMALE DURING THE ENTIRE OVIPOSITIONAL PERIOD

Initial laying date (1946)	Average temperatures during oviposition		Stocks tested							
			Southern California		Dinuba		Parlier I		Parlier II	
	Daily mean	At 7:00 p.m.	Number of females	Average number eggs per female	Number of females	Average number eggs per female	Number of females	Average number eggs per female	Number of females	Average number eggs per female
Apr. 20	67.3	75.9	74	62.9	125	62.9	35	74.3	....	....
June 11	73.6	84.0	111	84.0	120	46.2	50	48.1	..	....
June 29	79.6	89.7	...	....	150	47.2	...	....	..	....
July 10	81.9	91.2	250	121.3	111	76.8	100	79.8	..	....
Aug. 10	80.0	88.3	150	104.0	200	48.8	100	68.7	..	....
Aug. 29	71.7	77.5	199	134.1	150	63.8	...	....	..	....
Sept. 27	67.2	70.8	100	143.0	...	....	...	....	74	81.7
Total or weighted mean	....	....	884	114.1	856	56.5	285	69.7	....	....

for Parlier I and southern California moths (69.7/114.1 = 0.61). It therefore appears that the two Parlier stocks have similar laying tendencies.

A series of comparative tests were made with two stocks to determine how averages of the numbers of eggs laid are affected by infertile or otherwise unproductive females. For each test, 15 females of the Dinuba stock and 15 females of the southern California stock were placed, individually, in small cages containing 3 males. The cages were observed for 10 days, and separate records of eggs laid and hatched were kept for every female. In the nine tests summarized in table 7, the two stocks proved to be unlike in regard to the number of unproductive females observed. Every one of the southern California females laid eggs, whereas approximately 12.8 per cent of the Dinuba females failed to do so. The hatching records revealed deficiencies of another type. There were a few females that deposited only nonviable eggs. Presumably the latter were infertile, for embryos did not develop. Approximately 11.2 per cent of the Dinuba females and 4.5 per cent of the southern California females belonged in this category.

Estimates of the frequency of unproductive females, as furnished by this series of tests, provide a means of adjusting ovipositional averages to exclude the nonreproductive individuals. For example, the 113 Dinuba females deposited 8,712 eggs, or an average of 65.6 eggs per female for individuals of all categories, or 79.3 eggs per female for laying individuals. By further eliminating the 15 defectives of the second category, together with their total production of 113 eggs, the average is increased to 84.2 eggs per female for fertile females. Similarly, the 132 southern California females deposited 14,864 eggs to average 112.6 eggs per female for laying females. The 6 defectives laid 196 eggs, hence the average for the fertile females only was 116.4 eggs per female.

Although the unproductive females occurred with greater frequency in the less vigorously reproducing Dinuba stock, the differential effect of this phenomenon was not the sole factor responsible for stock differences in oviposition. There appeared to be some inherent difference in laying capacity, as attested by the average calculated for the fertile females, namely 84.2 eggs per female for Dinuba females and 116.4 eggs per female for the southern California females.

TABLE 7
SUMMARY OF 10-DAY OVIPOSITIONAL TESTS TO DETERMINE THE RELATIVE NUMBERS OF UNPRODUCTIVE FEMALES*

Date mated (1946)	Average temperature during oviposition		Number of females					
			Dinuba stock			Southern California stock		
	Daily mean	Maximum	Observed	Not laying	Laying only nonviable eggs	Observed	Not laying	Laying only nonviable eggs
Apr. 5	62.8	75.1	14	1	0	12	0	1
Apr. 22	68.3	85.2	15	1	0	15	0	1
June 3	69.0	83.8	15	2	0	15	0	0
June 14	74.6	89.9	15	4	3	15	0	1
June 23	75.6	89.8	14	1	3	15	0	0
July 6	78.9	94.3	15	1	1	15	0	0
July 23	80.4	93.6	15	1	3	15	0	0
Aug. 1	82.5	99.4	15	4	3	15	0	3
Aug. 13	79.3	95.3	15	2	2	15	0	0
Totals	....	....	133	17	15	132	0	6

* The pooled chi-square for stock differences in reproductive status of females—productive or unproductive, including deficiencies of both types—is significant; $\chi^2 = 18.88$, $P < 0.01$.

The temperature data of table 7 suggest that hot weather retards reproduction by increasing the number of unproductive females. That such is the case, however, is not apparent in the material presented earlier (tables 5 and 6).

VIABILITY OF THE EGGS

In the routine handling of eggs affixed to wax paper it was noticed that there was always a small percentage of eggs which did not hatch and, furthermore, that the percentage appeared to increase during hot weather. In view of the second observation, the percentages of eggs hatched were determined for relatively large batches of eggs incubated under varying conditions of summer temperature and humidity. As a check on the procedures involving wax paper, percentages of eggs hatched were also determined for eggs laid on peach leaves.

As a preliminary step in establishing procedures, information was desired as to the advisability of making up samples without regard to the ages of the ovipositing moths. Therefore data were assembled from available records of hatching and compiled as shown in table 8. The ages of the female moths are given in class intervals of 5 days; and the number of eggs deposited, together with the per cent hatched, are totaled for all of the females within each 5-day interval of age. The eggs having the lowest viability were deposited by females of the middle age class (11 to 15 days). This was also the age class in which the largest number of females ceased to oviposit. In other words, the females which laid for shorter periods contributed a larger proportion of nonviable eggs than those which laid for longer periods. The longer-lived

TABLE 8

HATCHABILITY OF EGGS CLASSIFIED ACCORDING TO AGE OF FEMALE MOTHS, 1946

Stock	Number of females	Age of females in days: 2–5	6–10	11–15	16–20	21–25
		Number of eggs laid / *Per cent of eggs hatched*				
Dinuba	169	2,319 / *82.4*	4,432 / *75.2*	3,062 / *69.8*	784 / *80.6*	153 / *85.6*
Southern California	75	4,339 / *94.8*	3,769 / *90.7*	1,724 / *72.2*	355 / *93.1*	40 / *97.5*

females continued to oviposit for periods ranging up to 25 days. The eggs deposited by these older individuals proved to be as viable as those deposited at the beginning of oviposition. The data imply that the variations in the hatching as revealed in table 8 are related to differences in vitality or physiological condition of the moths, as evidenced by the duration of oviposition and, possibly, by the size of the brood. In view of the drop in oviposition and in viability of eggs with females 11 to 15 days old, the eggs used in experiments to be described were taken only from cages containing moths 2 to 10 days of age.

In one series of tests, samples of eggs were incubated at various intervals during the change from cool to hot weather, between April 25 and August 10, 1946, in order to compare the percentages of eggs hatched on wax paper during incubation periods having different average temperatures. In each test, three samples of eggs, one for each of three stocks, were incubated under uncontrolled conditions in the insectary. Table 9 presents the results obtained from the hatching of 71,047 eggs. The tests are arranged in the table according to ascending order of average maximum temperatures during incubation.

The experiment summarized in table 9 showed that the viability of the eggs deposited on wax paper declined during the weather changes between spring and midsummer, and that the eggs deposited by three stocks of moths were similarly affected. The hatching of the eggs of the Dinuba stock declined 20.3 per cent, from a high of 94.8 per cent on June 11 to a low of 74.5 per cent on August 8. The decline in hatching for eggs of the southern California stock was 21.6 per cent, and for those of the Parlier I stock, 27.2 per cent. An inverse relation between percentages of eggs hatched and the average temperatures during incubation is evident in the data. In order to find which of the three sets of average temperatures gave the closest correlation with per cent of eggs hatched, coefficients of correlation (r) were calculated by using one set of temperature values at a time. The largest coefficients were obtained when the

TABLE 9
PERCENTAGES OF EGGS HATCHED ON WAX PAPER WHEN INCUBATED AT VARIOUS TEMPERATURES

Date laid (1946)	Temperatures of insectary during incubation			Dinuba stock		Southern California stock		Parlier I stock	
	Average maximum	Greatest maximum	Average daily mean	Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched
Apr. 25........	81.6	87	66.1	1,863	90.8	817	90.7	605	81.2
Apr. 23........	85.8	94	68.9	1,643	93.1	989	88.8	524	90.5
June 11........	86.8	89	70.7	961	94.8	2,785	94.3	1,633	94.8
June 12........	87.0	90	72.0	1,052	91.3	2,075	91.3	1,472	87.9
Apr. 20........	87.3	94	69.5	583	91.1	742	85.9	473	80.1
Apr. 21........	88.0	94	70.1	712	91.1	1,001	89.0	383	85.1
Apr. 22........	88.2	94	70.3	1,894	90.8	1,440	88.1	931	85.8
June 13........	88.2	94	72.8	1,554	92.6	3,019	90.2	618	89.6
July 12........	92.4	97	77.4	1,945	93.0	3,334	87.8	1,491	86.7
Aug. 12........	93.8	96	77.4	3,115	79.7	4,347	81.0	2,186	75.9
July 16........	97.3	100	83.1	2,764	87.7	3,761	82.0	3,692	84.5
Aug. 10........	97.3	101	81.8	3,012	87.0	2,678	84.7	2,015	80.0
Aug. 8........	99.7	101	84.2	1,774	74.5	3,771	72.7	1,393	67.6
Total or weighted mean.	......	......	......	22,872	88.3	30,759	85.9	17,416	83.8

Stocks	Degrees of freedom	Total chi-square
Dinuba–Southern California..........................	12	121.00*
Southern California–Parlier I..........................	12	108.87*
Dinuba–Parlier I....................................	12	223.72*

* $P < 0.01$.

average maximum temperatures were used as one set of variates. The average daily mean and the greatest maximum temperatures gave slightly lower coefficients (table 10).

The eggs of the three stocks appeared to differ in viability. The chi-square test was applied to the data of table 9 by computing a sum of chi-squares for the samples by considering two stocks (columns) at a time (see table 9).

A second experiment, similar to the first in method, was made to compare the percentages of eggs hatched when incubated on wax paper with the percentages hatched when incubated on peach leaves. The peach leaves were handled as bouquets of twigs having their cut ends plugged into vials of water. While the eggs were incubating, the twigs were kept in the insectary, shielded from the sun but not from air currents. The eggs on wax paper were also incubated under uncontrolled conditions in the insectary. Those used in each test were deposited on both leaves and wax paper by the same batch of moths, that is, the twigs and paper were placed in the same cage. Different batches of moths, southern California stock, supplied the eggs for tests set up on different dates.

In table 11 the results of fifteen tests are arranged in ascending order of average maximum temperatures during incubation. In view of possible differences in surface moisture and aëration, separate counts were made for eggs incubated on the upper and lower surfaces of the leaves. There are no stomata in the upper epidermis of peach leaves, whereas there are approximately 22,500 stomata per square centimeter in the lower epidermis (Miller, 1938).

TABLE 10

COEFFICIENTS OF CORRELATION BETWEEN PER CENT OF EGGS HATCHED AND TEMPERATURES DURING INCUBATION; DATA FROM TABLE 9

Temperatures during incubation	Coefficients of correlation		
	Dinuba stock	Southern California stock	Parlier I stock
Average maximum	−0.72	−0.82	−0.56
Average daily mean	−0.71	−0.78	−0.54
Greatest maximum	−0.59	−0.71	−0.53

The ranges of variation in percentages of eggs hatched during this experiment were noticeably less than those observed in the previous experiment, but the range of average temperatures during incubation was also smaller. The range of difference in viability was 9.7 per cent for eggs incubated on the lower leaf surfaces. For eggs incubated on the upper leaf surfaces the range was 11.8 per cent, and for eggs incubated on wax paper it was 11.2 per cent. The variations introduced into the experiment through the use of eggs laid by different batches of moths almost obscured the variations due to temperature differences. For example, the eggs incubated at the intermediate temperatures hatched in greater numbers than those incubated at the lower temperatures. In general, the percentages hatched in those tests made at the highest temperatures were but slightly below the weighted means for the experiment.

On the basis of the results obtained in the second experiment it is concluded that the viability of the eggs was not appreciably affected by midsummer weather conditions when they were incubated on living peach leaves.

The results further indicate that the viability was greater for eggs incubated on peach leaves than for those incubated on wax paper, and also that viability was slightly greater on the lower than on the upper surface of the peach leaves.

The mortality of the eggs incubated on wax paper in the second experiment was somewhat lower than in the first experiment or with previous observations. In the first experiment, the eggs were deposited in cages containing only small pads of wet cotton, one pad per cage. In the second experiment, they were laid in cages containing bouquets of transpiring peach twigs in addition to the wet pads. The amount of foliage was large in relation to the volume of the cages. The higher mortality shown in the first instance may mean that the eggs were especially susceptible to dry atmospheric conditions during the first few hours after being deposited.

In the first of the hatching experiments moderately good inverse correlations were obtained between percentages of eggs hatched on wax paper and the average maximum temperatures during incubation. This does not mean that the variations in hatching were due exclusively to temperature changes;

TABLE 11

PERCENTAGES OF EGGS HATCHED ON PEACH LEAVES AND ON WAX PAPER WHEN INCUBATED AT VARIOUS TEMPERATURES

Date laid (1946)	Temperatures of insectary during incubation			Lower surface of leaves		Upper surface of leaves		Wax paper	
	Average maximum	Greatest maximum	Average daily mean	Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched
June 18	91.6	101	76.2	1,181	92.5	211	93.4	622	88.8
July 22	92.5	97	82.0	2,648	93.8	1,886	92.6	885	90.2
July 23	92.5	97	81.8	2,059	94.9	1,106	92.5	913	90.4
July 12	92.6	97	77.5	1,679	94.8	974	94.1	1,059	89.3
July 11	93.0	99	78.2	1,896	94.8	1,388	94.7	1,384	89.8
July 13	93.6	100	77.6	1,871	94.0	798	95.4	634	90.4
July 28	93.8	101	78.3	2,361	96.1	924	94.7	1,098	93.1
June 17	94.2	101	77.6	1,034	90.6	459	85.5	442	85.8
Aug. 13	94.4	98	77.5	1,790	94.1	600	95.2	2,035	90.3
Aug. 14	94.8	98	77.9	2,317	93.5	959	94.6	2,254	89.0
Aug. 15	94.8	98	78.3	1,381	95.5	897	95.1	1,822	92.2
June 16	95.4	101	77.9	1,229	95.5	360	93.6	440	84.1
Aug. 5	96.4	101	80.2	1,448	86.4	1,308	83.6	1,170	81.9
Aug. 6	97.5	101	81.3	1,520	92.8	1,215	90.0	1,199	87.9
July 29	98.4	104	81.0	2,737	91.5	1,592	87.9	666	92.2
Total or weighted mean	....	....	....	27,151	93.8	14,677	92.1	16,623	89.3

Surface	Degrees of freedom	Total chi-square
Lower leaf–upper leaf	14	50.51*
Upper leaf–wax paper	14	132.20*
Lower leaf–wax paper	14	274.86*

* $P < 0.01$.

for, in general, increases in temperature were usually accompanied by decreases in relative humidity, and vice versa. Furthermore, the characteristics of the wax paper may have altered in the higher temperature ranges. Some information about the effect of differences in humidity on the viability of eggs adhering to wax paper was obtained from the following experiment. A large number of ovipositing moths were placed in a cage containing both wax paper and peach twigs. On the following morning the eggs on the twigs and paper were removed from the cages and immediately prepared for incubation. The twigs, already plugged into water-filled vials, were placed upright on a table in an open part of the insectary. The eggs affixed to the wax paper were divided into two portions and each portion was put into a shallow receptacle. One portion was put aside on a rack to incubate under uncontrolled conditions. The other portion was placed in a humidifier. The latter consisted of a battery jar partly filled with wet sand and a cover of muslin. While in use, the sand in the humidifier was kept wet to the point of saturation. Batches of eggs deposited by the same moths were treated in this manner for 3 days in succession (July 11, 12, and 13). The three batches of eggs were combined and treated as one lot (lot A, table 12). The procedure was repeated for three more batches (lot B) at a later time (August 13, 14, and 15).

The outcome of the experiment is shown in table 12. The percentages of eggs hatched on peach leaves were greater than the percentages hatched on

TABLE 12

PERCENTAGES OF EGGS HATCHED WHEN INCUBATED ON WAX PAPER UNDER CONDITIONS OF HIGH AND LOW HUMIDITY AND ON PEACH LEAVES, 1946

Lot	Temperatures of insectary during incubation			Average per cent relative humidity of insectary		Lower leaf surface		Wax paper in moist chamber		Wax paper in dry tray	
	Average maximum	Greatest	Average daily mean	Maximum	Minimum	Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched
A	95.1	100	79.6	87	27	5,446	94.5	7,969	90.4	3,069	89.7
B	94.3	96	77.8	88	27	5,488	94.2	7,658	92.7	6,111	90.4

Computed chi-square
($d.f.=1$)

Lower leaf surface and wax paper (humidified)		Wax paper (humidified) and wax paper (dry tray)	
A	75.57*	A	0.93
B	11.78*	B	23.12*

* $P < 0.01$.

either the dry or humidified wax paper. Also, in both trials, the percentages hatched on humidified wax paper were greater than the percentages hatched on wax paper under insectary conditions, although only one trial yielded a difference great enough to be significant. Increasing the moisture content of air surrounding the eggs on wax paper, from midsummer conditions to near saturation, resulted in some increase in the number of eggs hatched. Yet neither hatch obtained in the moist chamber equalled that obtained from eggs on the leaves. Probably surface temperature regulation by the leaves and surface ventilation are additional factors affecting the viability of eggs on leaves. The eggs on the leaves of the cut twigs probably developed at temperatures several degrees lower than the air temperatures in the interior of the insectary. According to Miller (1938), the temperature of leaves in direct sunlight, as measured on the upper leaf surfaces of several crop plants, are apt to fluctuate rapidly above and below the temperature of the air. In diffuse sunlight, however, the temperature of attached turgid leaves averages from 0.1° to 3.0° C below air temperatures (Miller and Saunders, 1923). It is further known that air currents tend to reduce leaf temperatures (Smith, 1909).

Eggs on wax paper were also less viable when incubated under uncontrolled conditions than when incubated with the egg side in contact with a layer of green peaches packed in muslin-covered wooden trays. The results of two replicate counts are given in table 13.

TABLE 13
PERCENTAGES OF EGGS HATCHED ON WAX PAPER IN DRY TRAYS AND IN TRAYS CONTAINING GREEN PEACHES

Date laid (1946)	Temperatures in insectary during incubation, ° F			Replicate	Dry trays		Over peaches		Chi-square (*d.f.* = 1)
	Average daily mean	Average maxi-mum	Greatest maxi-mum		Number of eggs observed	Per cent hatched	Number of eggs observed	Per cent hatched	
July 16.......	81.9	97.3	100	A	1,760	81.1	2,041	91.3	82.35*
				B	2,001	82.7	2,237	92.6	97.41*

* $P < 0.01$.

DISCUSSION

The question of the relation between the local summer climate and Oriental fruit moth propagation arose during 1944 and 1945, when the numbers of eggs deposited and the percentages of eggs hatched on wax paper were observed to decline considerably during hot weather. Moreover, marked increases in oviposition were noted when, during hot weather, the maximum temperatures (ranging from 92° to 107° F) were reduced approximately 10 degrees by the construction of evaporative cooling systems over the cages. Other observers have also commented on the adverse effect of high temperatures on oviposition. Garman (1930) found that the Oriental fruit moths in cages often suffer and may die without laying at temperatures above 90°. Snapp and Swingle (1929) observed that temperatures above 100° greatly reduce the number of eggs laid and that maximum laying occurs on days having a range of 70° to 95°. The optimum range for oviposition is given as 70° to 90° by Peterson and Haeussler (1930).

Averages of the number of eggs laid during 1944 and 1945 did not exceed 35 eggs per female for moths of the Dinuba stock. The larvae from which they were derived were reared on apples exclusively during 1944. During 1945, some of the larvae were reared on peaches but the majority were reared on apples, commercial Pippins (winter stored) in the spring months and small green fruit after thinning time. The cocooned larvae were not differentiated with respect to type of food or duration of feeding. They were taken from feeding trays as long as the fruit was not badly soured or contaminated with molds. All of the cocoons were put into a common emergence cage.

The crowding of larvae within the fruit also may have affected the size and fecundity of the moths. The wax papers to which the eggs adhered were cut and arranged on the apples or peaches so that about ten larvae would enter each of the fruits. Dustan's (1935) experiments indicate that the rearing of ten larvae per fruit impairs the fecundity of the adult females. When reared as two larvae per apple, adult females averaged 39 eggs each; but when reared as ten larvae per apple, the adult females averaged only 14.5 eggs each.

In the tests conducted during 1946, moths of the same stock deposited more eggs than before and, furthermore, oviposition did not break down in midsummer. The increased vitality during the third year was probably due to a change in the type of food used for rearing the larvae and to the selection of larvae for size and feeding time. Green peaches were used exclusively in 1946. It is more difficult to use peaches on a large scale because they are apt to decompose badly when infested with immature larvae, especially in hot weather. A standard procedure was adopted in which only the first larvae to emerge, the best in color and size, were withdrawn from the feeding trays. Those appearing in trays having partly rotten or molded fruit were discarded.

It now appears that the earlier results were due to inadequacies of the methods rather than to severe summer climate. Propagation of the Oriental fruit moth was maintained at a high level throughout the summer when the moths were obtained only from vigorous larvae reared on green peaches and when peach foliage instead of wax paper was used as an incubating medium for the eggs.

The most prolific of the insectary moths (southern California stock) laid 114.1 eggs as an average for 884 females. The highest average obtained for any one test was 143.0 eggs per female for 100 females. The average for the season is considerably greater than hitherto obtained for Oriental fruit moths by other observers, and yet it is believed to be a low estimate of the maximum production for the species under optimum outdoor conditions. High averages for single tests have been obtained in two other insectaries. In one test made by Peterson and Haeussler (1930) at Ironton, New Jersey, 100 females averaged 148 eggs each. At Wooster, Ohio, Neiswander (1936) reported an average of 129.0 eggs per female from three cages each containing 10 females. Steiner and Yetter (Yetter and Steiner, 1931; Steiner and Yetter, 1933) estimated Oriental fruit moth reproduction by determining the egg content of 750 dissected females. The average number of eggs in preovipositional females was 141 eggs in 1931 and approximately 200 in 1932. The maximum number of eggs found in any one female was 362. They found no evidence that additional immature eggs form after the first day of adult life. The higher counts during 1932 were thought to be one of the causes for a heavier orchard infestation during that year.

The work leading to the differentiation of several stocks of moths was done as a routine check on the original stock of insectary moths to determine whether there were genetic differences in responsiveness to hot-weather conditions. The fact that two stocks differed in oviposition and three stocks in viability of eggs is of problematic significance. The differences may have originated as genetic segregations in consequence of laboratory procedures in breeding. On the other hand, it may mean that the populations from which the samples were taken differ in reproductive potential and that they have not yet intermingled.

SUMMARY

Oriental fruit moths were found to mate successfully as early as the day of emergence. Individuals of both sexes appeared to retain the ability to reproduce after remaining unmated for relatively long periods of time. One male usually mated successfully with only one female during one 12-hour

period of association, although in the same period additional females present were occasionally induced to lay small numbers of nonviable eggs. Females inseminated by one or more males during one 12-hour period of association oviposited normally thereafter in the absence of males.

Comparative ovipositional tests were made for two stocks of moths, one obtained from Orange County, in southern California, and the other from Dinuba, in central California. When reared and tested under the same conditions, females of the southern California stock deposited, as an average, about twice as many eggs as the females of the Dinuba stock. Oviposition tests were also made for two additional stocks, Parlier I and Parlier II, but they were not clearly differentiated from each other or from the Dinuba stock.

The average numbers of eggs deposited by females during 7-day laying periods were compared for groups of females laying at different times between April 18 and September 9, 1946. The data show that two of the three stocks tested (southern California and Dinuba) gave the highest production averages during the hottest part of the summer, July 10 to August 8. Moths of the third stock (Parlier I) oviposited about as well in hot weather as in cool weather.

When eggs affixed to wax paper were incubated under uncontrolled conditions, the percentages hatched were found to vary inversely with the average temperatures during incubation. For eggs deposited by moths of three stocks, the highest percentages hatched in individual samples were approximately 95 per cent, whereas the percentages hatched in samples incubated at the highest average summer temperatures ranged from 74.5 per cent for eggs of the Dinuba stock to 67.6 per cent for eggs of the Parlier I stock.

There were significant differences in the viability of eggs laid by moths of the three strains.

During hot weather, the percentages of eggs hatched after being incubated on living peach leaves were greater than the percentages obtained for eggs incubated on wax paper under laboratory conditions. The percentages ranged from 96.1 to 83.6 for samples of eggs incubated on peach leaves as compared with a range of 93.1 to 81.9 for samples of eggs incubated on wax paper. The viability of eggs incubated on wax paper was slightly increased by increasing the atmospheric moisture. The viability of eggs deposited on the lower surfaces of peach leaves was slightly greater than the viability of those incubated on the upper surfaces.

The viability of eggs incubated on peach leaves was not greatly reduced by hot-weather conditions: more than 90 per cent of the eggs hatched in 26 out of 30 samples (36,430 out of 41,237 eggs) which were incubated during the period June 16 to August 15, 1946.

Evidence was obtained to show that differences in atmospheric moisture account only in part for differences between the percentages of eggs hatched on dry wax paper and on transpiring peach leaves.

From these experiments it does not appear that propagation of the Oriental fruit moth is seriously impaired by the high temperature and low humidity factors in the summer climate of central California.

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