EFFECT OF LARVAL DENSITY ON THE DEVELOPMENT OF Aedes aegypti (L.) AND THE SIZE OF ADULTS*

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The effect of larval density of Aedes aegypti *(L.) on larval development and the size of resulting adults was studied in the laboratory. High larval mortality, long larval period, and small size of resulting adults were observed, when the larval density was high, as well as when the amount of food was small. Although the high larval density is often associated with shortage of food, it was demonstrated that even only the high larval density could produce these phenomena, when the amount of food per larva was kept constant. The effect of the density is considered to be expressed through increased stimulation of larvae by mutual contacts.*

INTRODUCTION

The effect of population density on the physiology and ecology of insects has received much attention by many investigators, as it is of basic importance in the study of population dynamics. As for mosquitoes, it is known that high larval densities are associated with high larval mortality, prolongation of the larval period, and small size of resulting adults with *Aedes aegypti* (L.) (Bar-Zeev, 1957; Shannon and Putnam, 1934), *Anopheles gambiae* Giles (Gillies and Shute, 1954), and *Anopheles quadrimaculatus* Say (Terzian and Stahler, 1949). Also Spielman (1957) and Krishnamurthy and Laven (1961) reported that overcrowding larvae of *Culex pipiens* L. f. *molestus* reduces the rate of autogeny among the resulting adults, and Gillies and Shute (1954) mentioned the change in maxillary index of *Anopheles gambiae* by larval overcrowding.

Although high larval density, or overcrowding, is often accompanied by a shortage of food, it seems to be advisable to separate the effect of density itself from that of starvation, since the two could be quite different processes. Shannon and Putnam (1934) seem to have made their experiments by increasing the larval density and keeping the food amount per container constant. If so, it is very likely that the larvae in high density were affected not only by the density itself, but also by the shortage of food. Bar-Zeev (1957) used a constant amount of food per larva in his experiments to demonstrate the effect of larval density, and said, "When the amount of food was not too high, and therefore, no film was formed, there was no undue mortality under crowded conditions; however, the development of the larvae was greatly delayed". This seems to have indicated the effect of density. However, he added "The growth rate was normal, provided that the amount of food per larva was

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adequate, and that the water was renewed so as to prevent the development of a film of yeast. It can, therefore, be concluded that the inhibitory effect of crowded conditions on larval development is due to lack of food".

Thus it seems that no conclusion has been established for the effect of larval density itself in mosquitoes, and therefore, it was considered worthwhile to explore this further.

The effect of density would be investigated in an experiment with a constant quantity of food per individual at varying density levels (Klomp, 1964). On the other hand, if the quantity of food per container is kept constant, the larvae at high density will suffer shortage of food particularly in the latter part of development, as well as the effect of high density. In order to recognize the effect of food quantity free from the effect of density, food quantity would have to be changed at the same density level.

METHOD OF EXPERIMENTS

The mosquitoes used were *Aedes aegypti* kept at the Department of Entomology, University of Alberta. The eggs, not older than 15 days from oviposition, were allowed to hatch in water with a small quantity of dried yeast (Fleichmann's). The larvae which hatched within 12 hours were put into cups with 100 ml water containing dried yeast or rabbit pellets (North West Mill and Feed Co., Ltd.) or both. These cups were kept at constant temperatures, and the observations were made at a certain time every day. At each observation time, distilled water was added to keep a constant volume. When pupation occurred, the pupae were put into water in small glass vials with cotton plugs after recording their number, and emergence was awaited.

Four experiments were performed.

Experiment I– This was preliminary in nature. Density range was 1 to 64 larvae per cup, food used was yeast with quantity range of 1 to 64 units (1 unit = 1.7 mg) per cup, temperature, 25.7 ±1.5 C.

Experiment II– In this experiment, the quantity of food per cup was kept constant at various density levels. Density range was 1 to 128 larvae per cup, food used was 64 units of yeast plus 100 units of rabbit pellets per cup, temperature, 29.8 ± 1.2 C. From this experiment, the combined effect of food quantity and larval density will be seen.

Experiment III– This experiment was done to see the effect of different foods, that is 64 units yeast, 100 units rabbit pellets, 64 units yeast plus 100 units rabbit pellets, and 64 units yeast plus 200 units rabbit pellets. Density was kept constant at 16 larvae per cup, temperature, 29.8 ± 1.2 C.

Experiment IV – In this experiment, the quantity of yeast per larva was kept at 1 and 4 units, density range 1 to 256, temperature, 26.3 ± 0.9 C. Thus the effect of larval density will be seen from the data based on series of density levels at constant food quantity per larva. Also, by comparing in the same density level, the effect of food quantity will be demonstrated.

RESULTS OBTAINED

Effect of Larval Density on Larval and Pupal Mortalities

The larval and pupal mortalities in Experiments I, II, III, and IV are given in Tables 1, 2, 3, and 4, respectively.

In Experiment I, low larval mortality was observed at the density levels of 1 and 4 larvae per cup, when 4 to 64 units of yeast were supplied to each cup. With increasing density particularly when the amount of yeast was small, larval mortality became higher. No pupation occurred in the density 16 with 4 units of yeast per cup or in the density 64 with 4 or 16 units. No appreciable tendency was recognized in pupal mortality.

TABLE 1 - Mortalities of *Aedes aegypti* larvae and pupae reared at different densities with different amounts of yeast (Experiment I).

Density	Yeast (units)* per cup	Yeast (units)* per larva	No. of repl.	Total no. of larvae	Larval mort. (%)	No. of pupae ♂	No. of pupae ♀	No. of pupae Total	Pupal mort. (%)
1	4	4	6	6	0.0	3	3	6	16.7
1	16	16	6	6	0.0	4	2	6	0.0
1	64	64	6	6	0.0	3	3	6	0.0
4	4	1	4	16	18.7	8	5	13	0.0
4	16	4	4	16	18.7	6	7	13	15.4
4	64	16	4	16	25.0	9	3	12	0.0
16	4	1/4	1	16	100.0	0	0	0	-
16	16	1	1	16	43.7	4	5	9	22.2
16	64	4	1	16	12.5	6	9	15	6.7
64	4	1/16	1	64	100.0	0	0	0	-
64	16	1/4	1	64	100.0	0	0	0	-
64	64	1	1	64	54.7	20	9	29	3.4

* 1 unit = 1.7 mg

Experiment II gave generally high pupation rate throughout the density levels of 1 to 128, indicating that the food used, 64 units yeast plus 100 units rabbit pellets, is suitable for larval survival. However, the larval mortality is lower at density 16 than at other densities, and this seems to indicate the optimum density for larval survival, with this combination of quantity and quality of the food.

TABLE 2 - Mortalities of *Aedes aegypti* larvae and pupae reared at different densities with a constant amount of food per cup (Experiment II).

Density	Replicates	Total no. of larvae	Larval mortality (%)	No. of pupae ♂	♀	Total	Pupal mortality (%)
1	23	23	13.0	12	8	20	5.0
4	12	48	6.2	21	24	45	4.4
16	5	80	1.2	43	36	79	1.3
64	3	192	3.6	100	85	185	1.6
128	2	256	16.4	126	88	214	0.9

Food used: 64 unit yeast plus 100 unit rabbit pellets per cup (1 unit = 1.7 mg).

Experiment III, where the density of larvae was 16 per cup, shows that larval and pupal mortalities decrease from 64 units yeast to 64 units yeast plus 200 units rabbit pellets. This means that the lower food shown in the table is the better food for larval and pupal survival.

TABLE 3 - Mortalities of *Aedes aegypti* larvae and pupae reared with different foods (Experiment III).

Food used*	Replicates	Total no. of larvae	mortality (%)	No. of pupae ♂	♀	Total	Pupal mort. (%)
Y64	2	32	12.5	12	16	28	7.1
R100	2	32	9.4	15	14	29	3.4
Y64 + R100**	5	80	1.2	43	36	79	1.3
Y64 + R200	2	32	0.0	19	13	32	0.0

Density: 16 larvae per cup.
*Y: yeast; R: rabbit pellets; accompanied figure: quantity per cup in units (1 unit = 1.7 mg).
**Data are from Table 2.

In Experiment IV, two series of the amount of yeast, that is 1 and 4 units per larva, were used. When the density was 16 or less, fairly high pupation was obtained, though the mortality is slightly higher with 1 unit yeast per larva than with 4 units. In density 64 with 1 unit yeast per larva, that is 64 units per cup, larval mortality was more than 50%, and only males pupated. In the density of 256 with 1 unit yeast per larva, that is 256 units per cup, larval mortality further increased up to 87%, 40% of pupae failed to emerge, and very low proportion of females was obtained. Very high larval mortality was observed also in the density of 256 with 4 units of yeast per larva, that is 1024 units per cup. This amount of yeast seemed to be too much for 100 ml water, because a film was formed on the water surface and high mortality occurred in earlier instars, unlike other combinations of density and food amount. Thus such a very low pupation rate as 2.9% is not due to the effect of high larval density, but probably to the film formation or other unfavorable conditions of the culture medium.

TABLE 4 - Mortalities of *Aedes aegypti* larvae and pupae reared at different densities with 2 series of a constant amount of yeast per larva (Experiment IV).

Density	Yeast (units)* per cup	Yeast (units)* per larva	No. of repl.	Total no. of larvae	Larval mort. (%)	No. of pupae ♂	No. of pupae ♀	No. of pupae Total	Pupal mort. (%)
1	1	1	32	32	9.4	18	11	29	3.4
4	4	1	13	52	20.8	23	19	42	7.1
16	16	1	5	80	13.7	44	25	69	1.4
64	64	1	2	128	57.8	54	0	54	1.9
256	256	1	2	512	86.9	64	3	67	40.3
1	4	4	32	32	12.5	20	8	28	3.6
4	16	4	13	52	0.0	27	25	52	0.0
16	64	4	5	80	13.7	42	27	69	2.9
64	256	4	2	128	23.4	60	38	98	5.1
256	1024	4	2	512	97.1	8	7	15	0.0

* 1 unit = 1.7 mg

In short, larval mortality generally increases with increased density and decreased food quantity through the shortage of food and the larval density itself. There seems to be an optimum density for larval survival, which differs from the minimum density. If the conditions are not suitable, then the favored sex is the male.

Effect of Larval Density on Pupation Curve

Frequency curves of pupation by sex in four experiments are shown in Figs. 1, 2, 3, 4, and 5. Males pupated earlier than females throughout the experiments. Generally a shorter larval period is seen in the cups where the density is lower and the amount of yeast is larger. When larval periods are compared on the basis of the same density with different amounts of food (see Fig. 1; compare Figs. 4 and 5), a longer larval period is seen with the decreased amount of food.

When the amount of food per larva was kept constant and the density of larvae was increased, the delay in development is clear, as seen in Experiment IV (Figs. 4 and 5). This is attributable to the effect of high larval density, not to the shortage of food, because the comparisons were made on the basis of the same amount of food per larva.

Here, it is apparent that the larval development is affected not only by the quantity of food, but also directly by the larval density, and the effect is more remarkable, when the amount of food per larva is smaller.

It is interesting that the longer larval period is usually associated with increased variation in larval period and with a tendency to be skewed towards the right. If a pupation curve is normally distributed, then it is expected that a cumulative percentage frequency of pupation in probit will be linear. Now, the normality of the pupation curves in Experiments II and IV, in which a fairly large number of larvae was used, was examined.

Cumulative percentage pupation in probit is plotted against larval period (days) in Figs. 6 to 11. When the density is low and food amount is large a linear relation is seen, that is, those pupation curves are shown to follow the normal distribution. The deviation from the normal distribution becomes remarkable with increasing density and decreasing food quantity. Thus there is some deviation from the normal distribution in the pupation curve, particularly when the conditions are unfavorable for larval development. Even when conditions are good, a few individuals sometimes pupate very late. For this reason, it seems that the median is a better representative of larval period than the mean.

Effect of Larval Density on Larval and Pupal Periods

Figs. 12, 13, and 14 show the relation between median larval period and larval density per cup for Experiment I, II, and IV, respectively. In these figures, the points with the same amount of food per cup were connected by straight lines. Generally, the median larval period becomes longer with increasing larval density. This is rather natural, because the amount of food per larva decreases with increasing density.

By connecting the points with the same amount of food per larva, the data for Experiments I and IV are represented in Figs. 15 and 16. In density levels of 256 and 64 of Experiment IV, a longer median period was obtained than in 1, 4 or 16, in spite of the

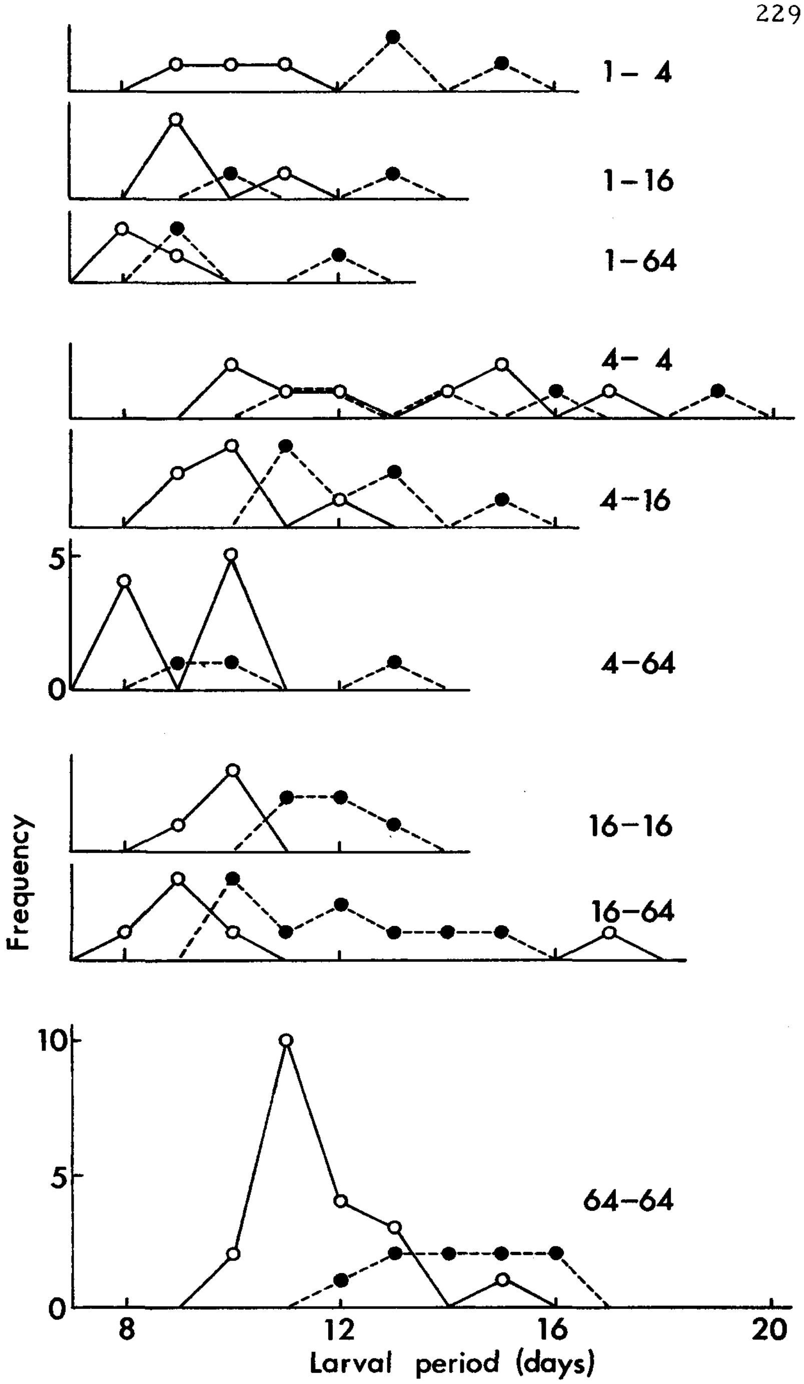


Fig. 1. Frequency distributions of larval period of *Aedes aegypti* (Experiment I). 4-64, for example, indicates that the larval density is 4 and the amount of yeast is 64 units per cup. ○ : males; ● : females.

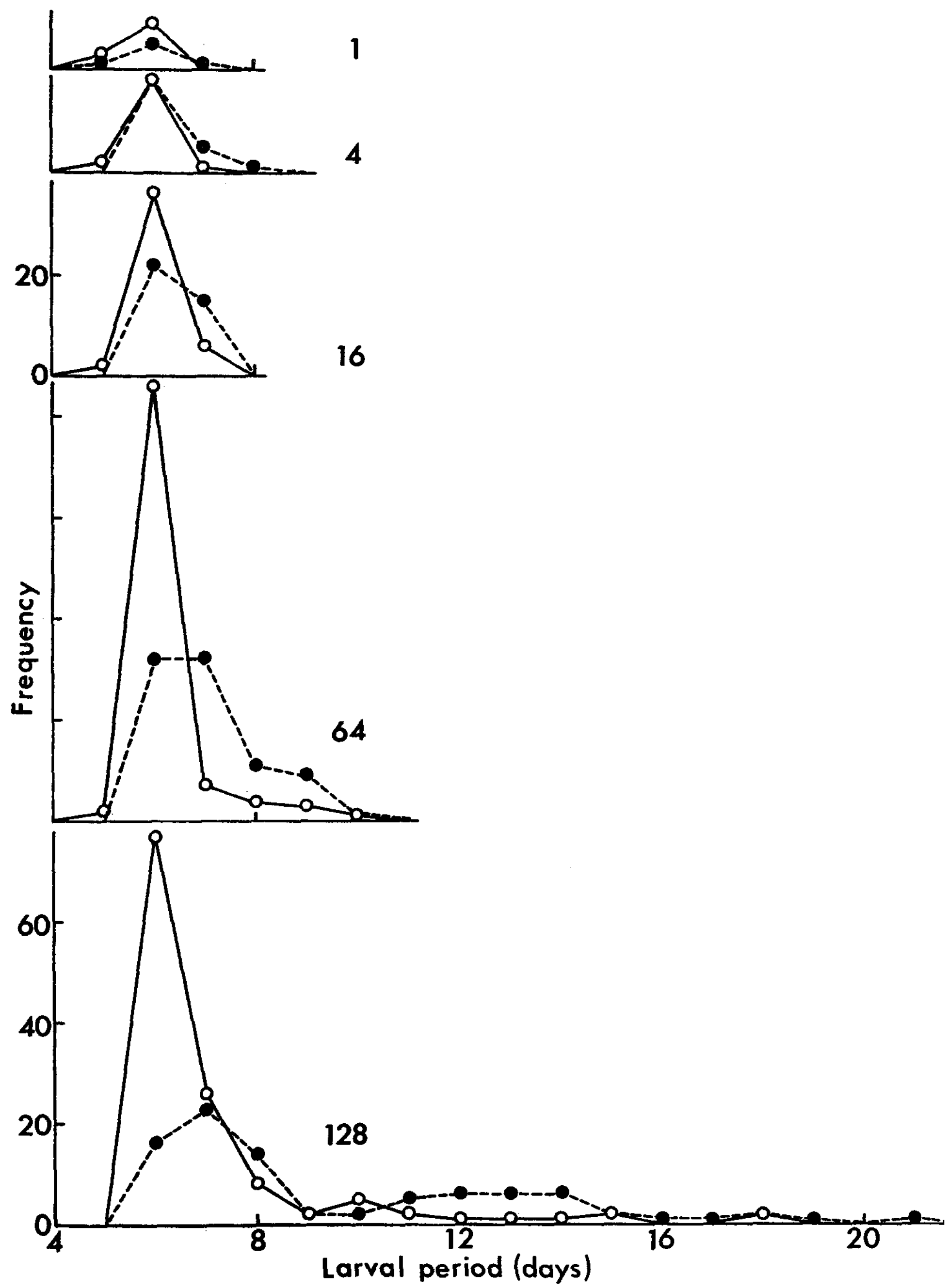


Fig. 2. Frequency distributions of larval period of *Aedes aegypti* (Experiment II). Figure shown indicates larval density. ○ : males; ● : females.

fact that the amount of food available for each larva in higher densities is the same as, or even slightly larger than, in lower densities. Here, the effect of high larval density is again suggested. Also in Experiment I, the tendency of the median to increase is seen at the density levels of 64 or more. It is interesting that there seems to exist a valley in median larval period at density 16, particularly

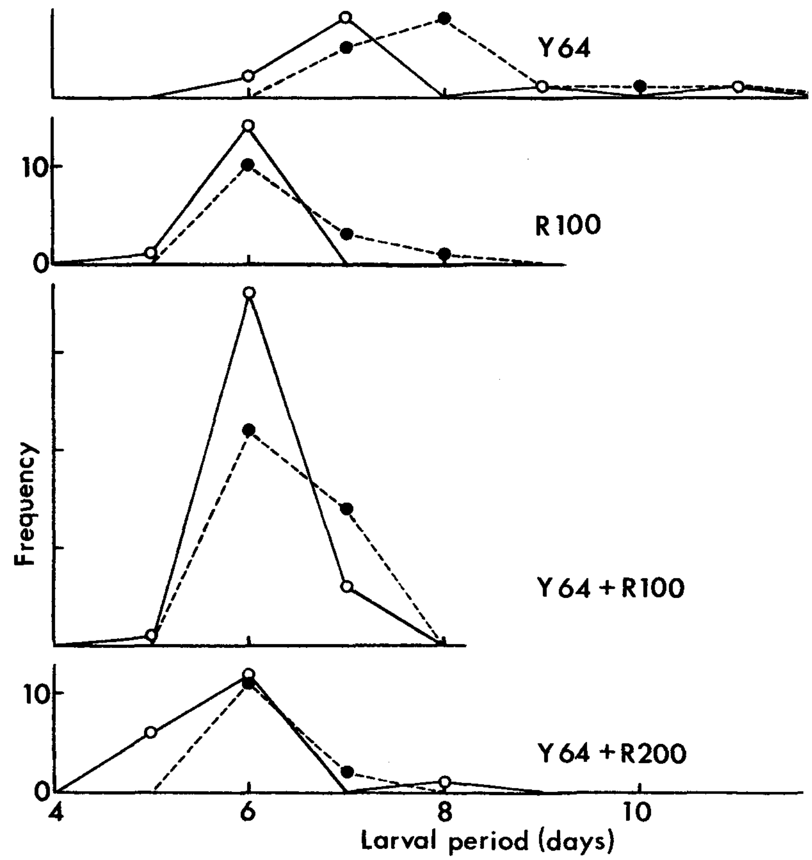


Fig. 3. Frequency distributions of larval period of *Aedes aegypti* (Experiment III). Y and R and accompanied figure indicate yeast and rabbit pellets and their amount in units. ○ : males, ● : females.

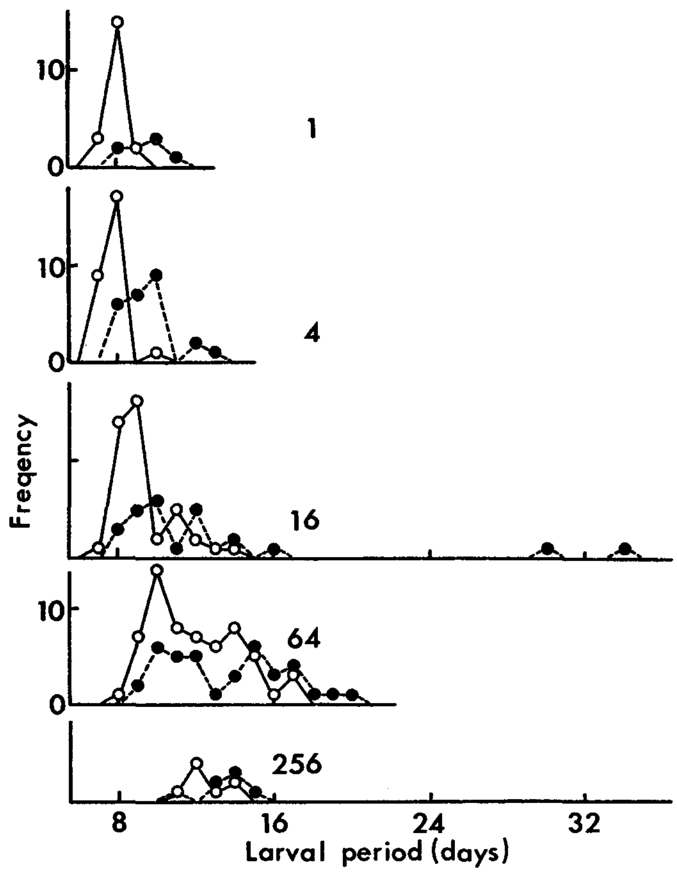


Fig. 4. Frequency distributions of larval period of *Aedes aegypti* (Amount of yeast per larva: 4 units; Experiment IV). Figure shown indicates larval density. ○ : males; ● : females.

when the amount of food is small, and furthermore, in the food amount of 1 in Experiment IV, the median becomes again smaller at density 1 than 4. The reasons for such peculiarities of the curves are not clear, but it seems that the median is determined by a balance between the effects of larval density and the amount of food available, and perhaps some other factors.

No distinct difference in pupal period was recognized among various amounts of food nor among larval density levels, though pupal density may affect the period. It seems that the pupal period is affected only by temperature, or at least, if some other factors affect it, their effect is very small. In Table 5, mean pupal periods in days are given by sex at the three different temperatures. The female has a slightly longer pupal period than the male.

It would be practically right to suppose that the larval period is determined by temperature, larval density, and the conditions of culture medium such as the quality and quantity of food, but the pupal period is determined only by temperature. The ratio of larval period seems, then, to indicate the suitability of the conditions for larval development. This ratio may be used to compare the larval period, even when experiments were made at different temperatures.

The calculated values for the ratio are shown in Tables 6 and 7, and compared on the basis of the same combinations of larval density and food amount in different experiments. The ratios for the combinations of D1Y4 (density 1 larva per cup, yeast 4 units per cup), D4Y16, and D16Y64 agree quite well among experiments, but those for D4Y4, D16Y16, D64Y16, and D64Y64, are rather

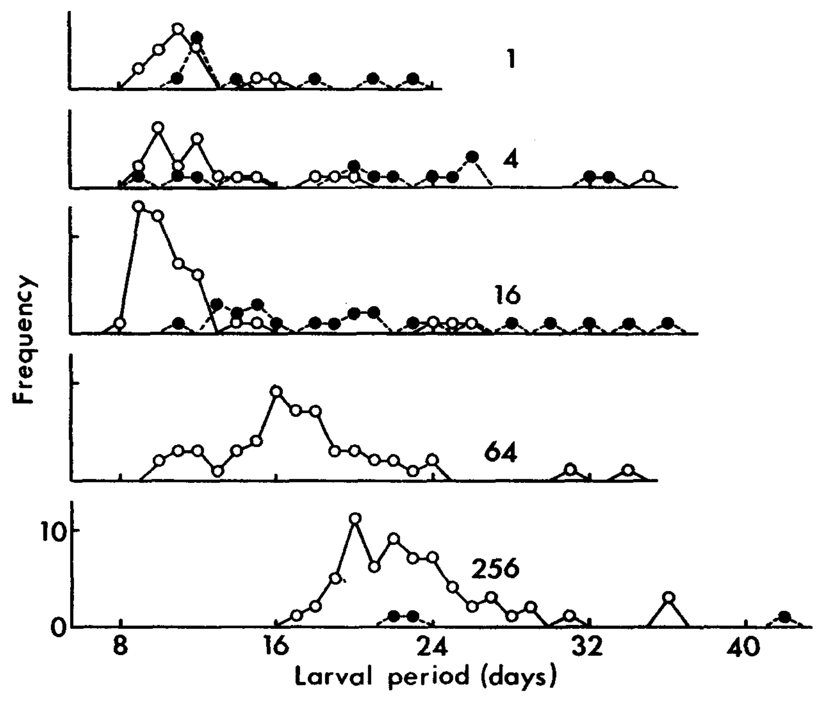


Fig. 5. Frequency distributions of larval period of *Aedes aegypti* (Amount of yeast per larva: 1 unit; Experiment IV). Figure shown indicates larval density. O : males; ● : females.

different from one another. The number of larvae used in Experiment I was not sufficient, and the latter combinations are considered somewhat unsuitable so that very slight differences in the conditions will make rather great changes in larval development. These would be responsible for rather great difference of the ratios in the latter group of combinations.

The above procedure will be valid only if the ratio of larval period to pupal period is constant over a reasonable temperature range. For this reason, further studies are required to determine the usefulness of the ratio. However, it is clear from the tables that larval period varies greatly with the quantity and quality of food at the same density level, and also that the same amount of food per cup, or even per larva, does not give the same larval period at different density levels. Therefore, care should be taken in attempting to determine the larval period at a certain temperature, or the developmental zero of mosquito larvae by rearing them at different temperatures.

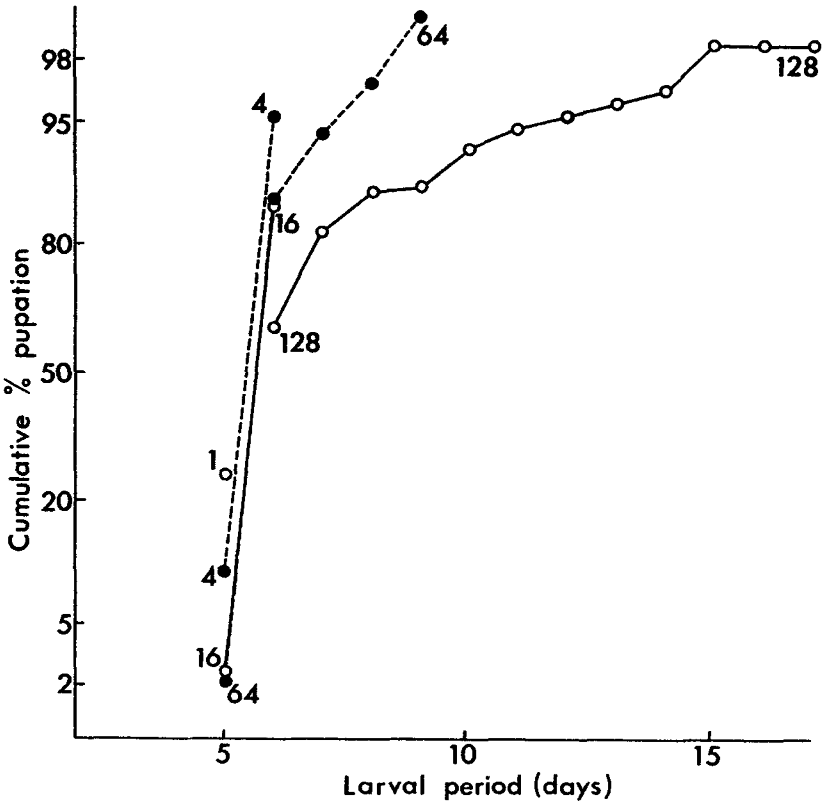


Fig. 6. **The relation between cumulative percentage pupation (probit scale) and larval period in males of *Aedes aegypti* (Experiment II). Figure shown indicates larval density.**

Effect of Larval Density on Body Size of Resulting Adults

In Figs. 17 and 18, the frequency distributions of wing length of the resulting adults in Experiments II and IV are given.

In Experiment II (Fig. 17), the wing length increases in both sexes slightly from density 1 to 16 larvae per cup, and decreases greatly with increasing density from 16. Fig. 18 shows the similar situation in Experiment IV, except for density 256 with yeast 4 units per larva, where the wing length is not considered to reflect the effect of this density, owing to high larval mortality in the earlier instars, as mentioned earlier. However, the changes in wing length are less remarkable than in Experiment II. This is due to the fact that the quantity of food per cup was kept constant in Experiment II, on the other hand in Experiment IV the quantity per larva was kept constant. Nevertheless, the apparent effect of larval density on the wing length can be seen in Experiment IV (Fig. 18).

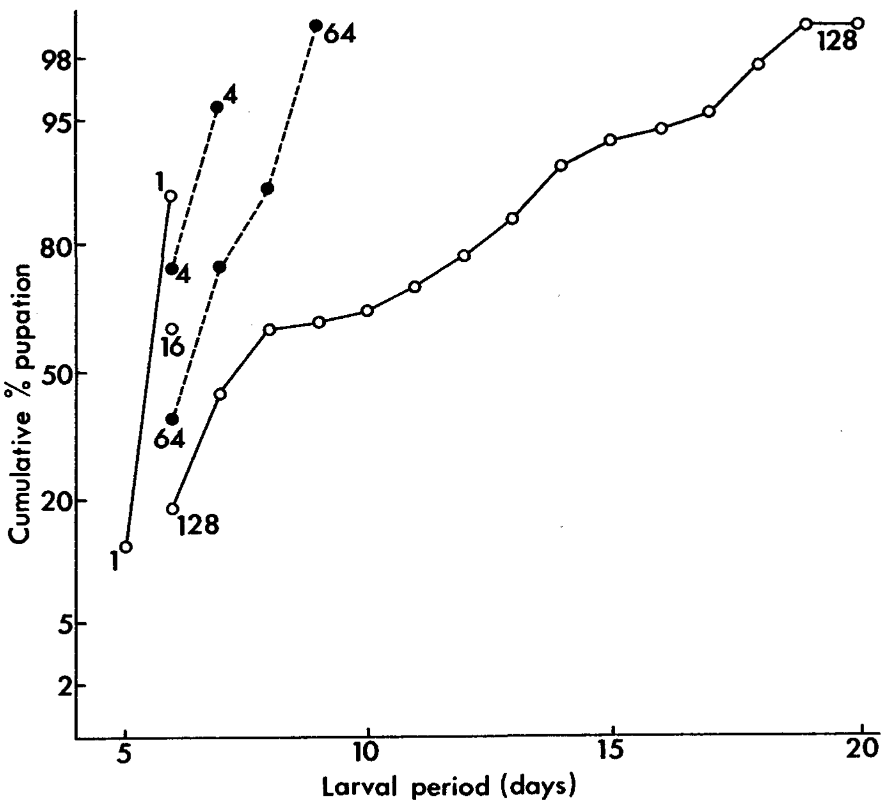
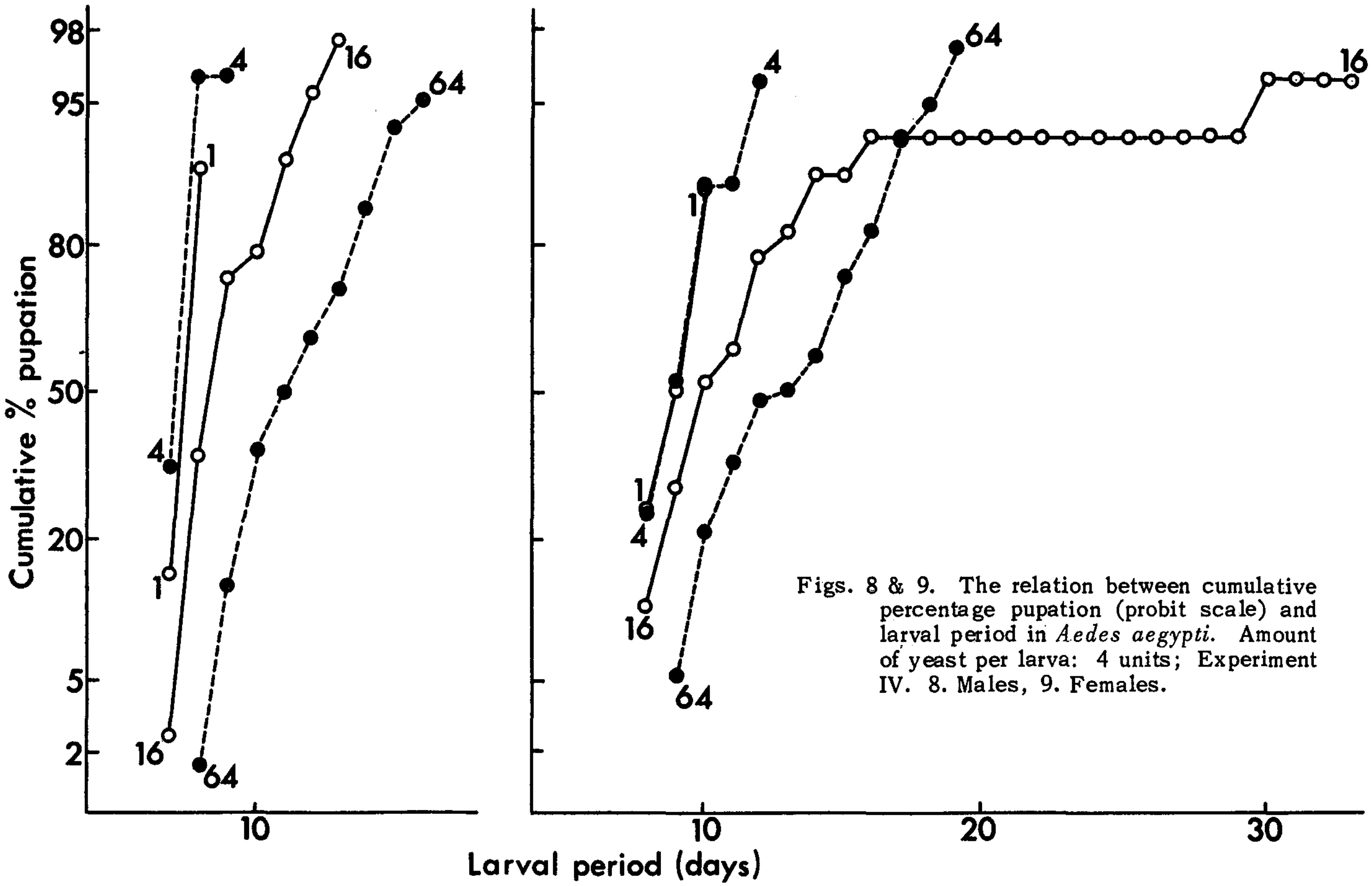


Fig. 7. The relation between cumulative percentage pupation (probit scale) and larval period in females of *Aedes aegypti* (Experiment II). Figure shown indicates larval density.



Figs. 8 & 9. The relation between cumulative percentage pupation (probit scale) and larval period in *Aedes aegypti*. Amount of yeast per larva: 4 units; Experiment IV. 8. Males, 9. Females.

It seems that the wing length of females is more sensitively affected than that of males with decreasing suitability for the larval stage, so that considerable overlapping in wing length of both sexes appears, as for example between densities 64 and 128 in Experiment II (Fig. 17). When the conditions become still less suitable, only males will pupate, as indicated from the densities 64 and 256 with yeast 1 unit per larva.

It is interesting that the frequency curve becomes steeper at the right hand side with decreasing suitability in the conditions for larval development, but the reasons for this are not yet clear.

Figs. 19 and 20 show the frequency curves of thorax length in Experiments II and IV. The thorax length shows a similar tendency to the wing length, excepting that the steepness of the curves at the right hand side is not seen, when the conditions become unfavorable.

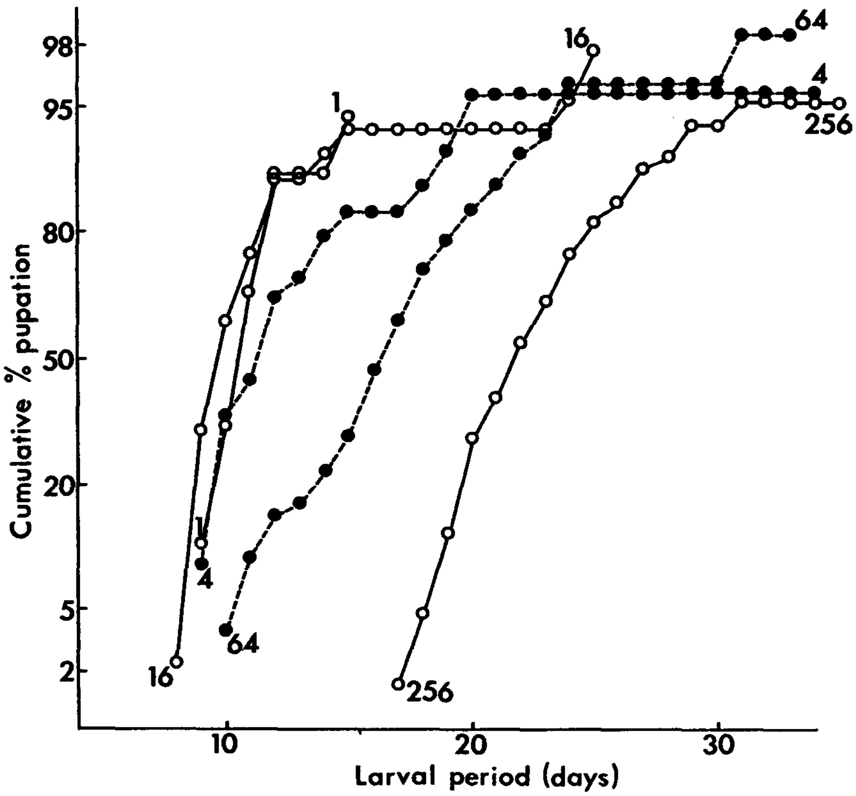


Fig. 10. The relation between cumulative percentage pupation (probit scale) and larval period in males of *Aedes aegypti* (Amount of yeast per larva: 1 unit; Experiment IV). Figure shown indicates larval density.

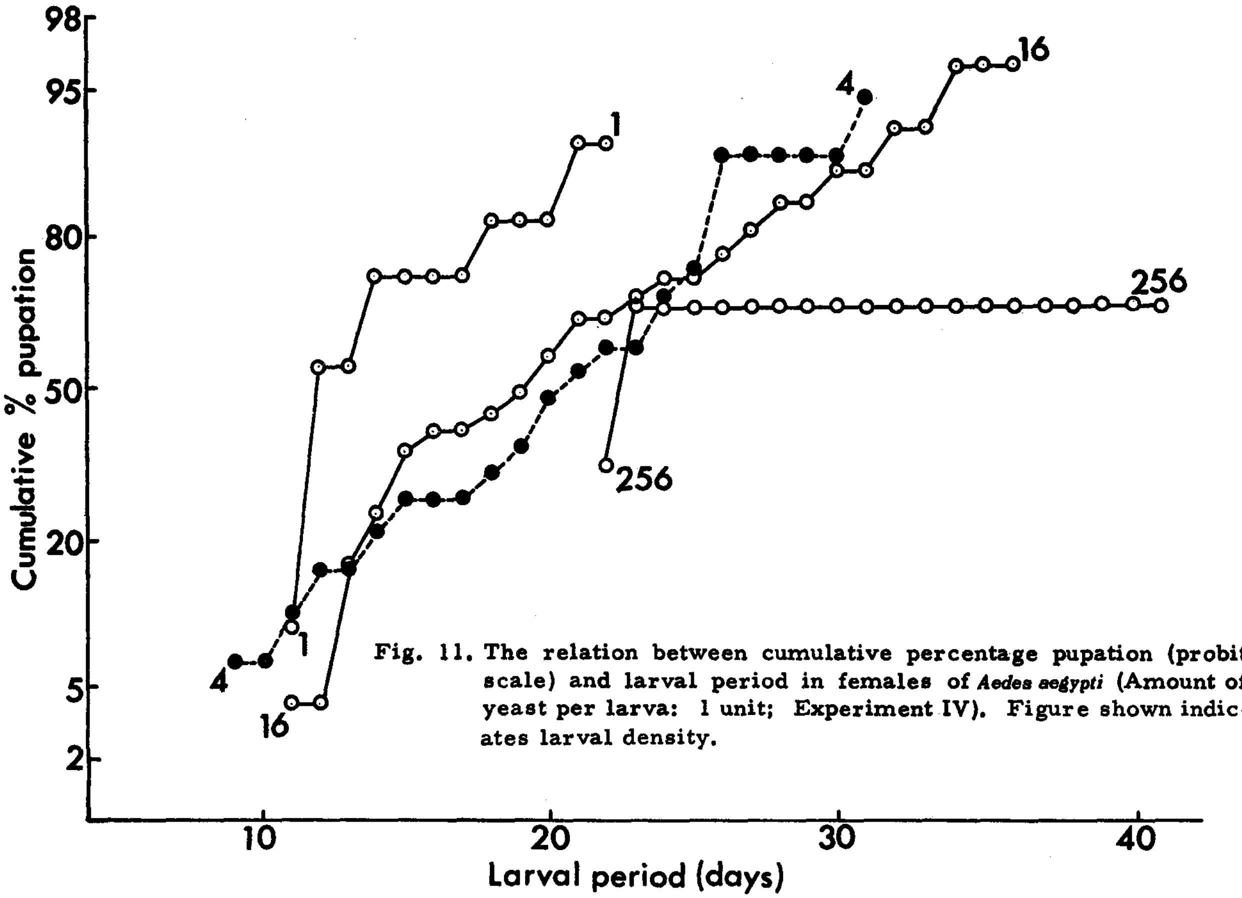


Fig. 11. The relation between cumulative percentage pupation (probit scale) and larval period in females of *Aedes aegypti* (Amount of yeast per larva: 1 unit; Experiment IV). Figure shown indicates larval density.

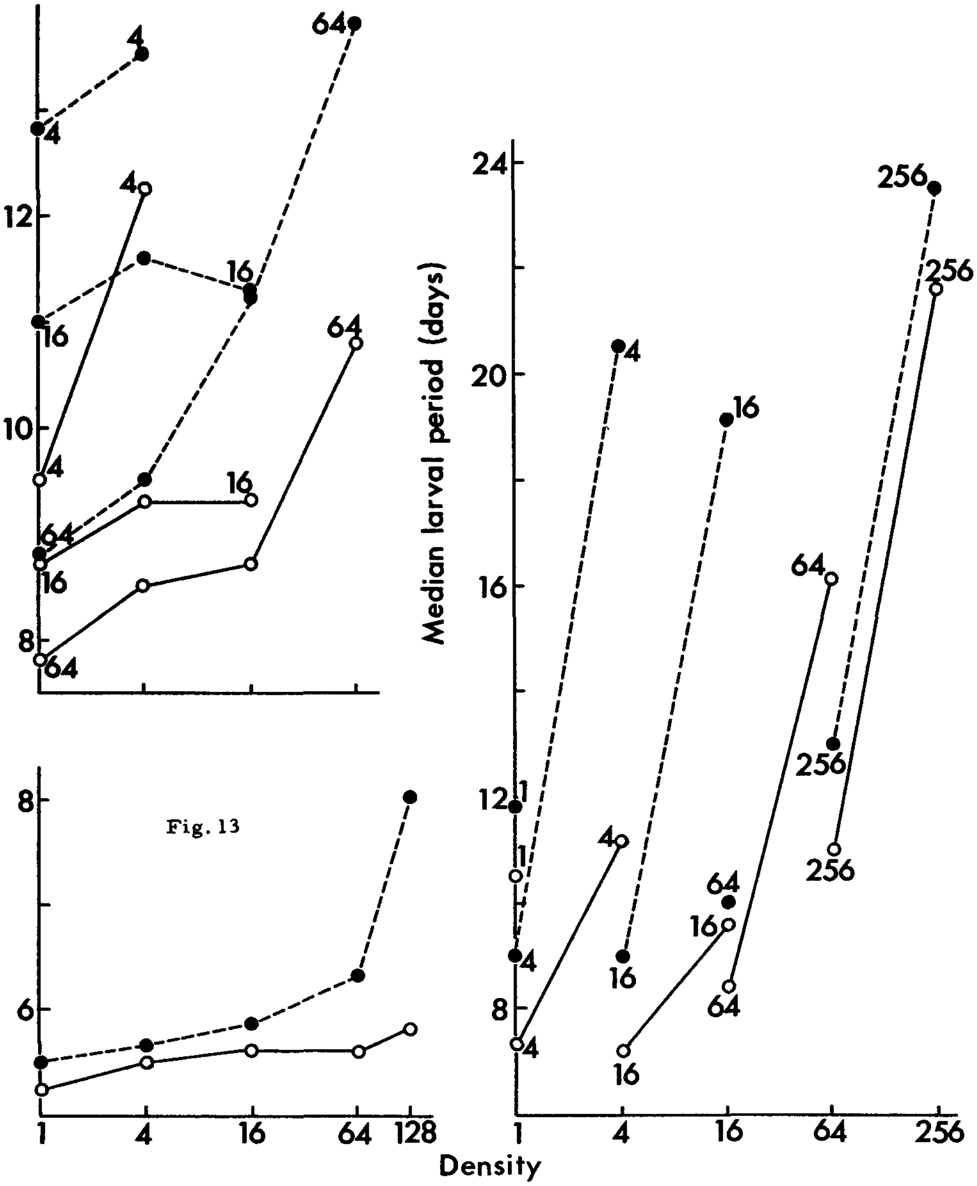
TABLE 5 - Pupal periods of *Aedes aegypti* by sex at different temperatures.

Experiment	Temperature C	Mean pupal period (days) Male	Female
I	25.7	2.76	2.78
II and III	29.8	1.83	1.94
IV	26.3	2.36	2.42

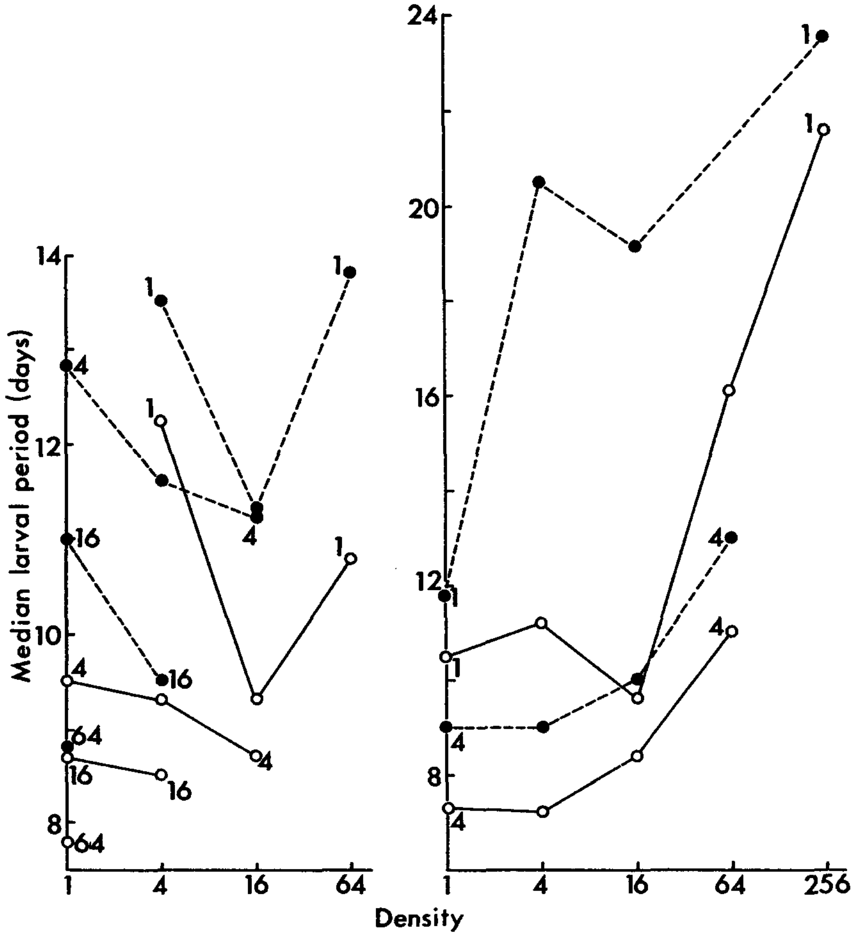
TABLE 6 - The ratio of larval to pupal period of the males of *Aedes aegypti* (Experiments I - IV).

Density	Food used*	Exp. I	Exp. II	Exp. III	Exp. IV	Mean
1	Y1				4.45	4.45
	Y4	3.44			3.14	3.28
	Y16	3.15				3.15
	Y64	2.83				2.83
	Y64 + R100		2.92			2.92
4	Y4	4.53			4.79	4.66
	Y16	3.37			3.05	3.21
	Y64	3.08				3.08
	Y64 + R100		3.01			3.01
16	Y4	**				**
	Y16	3.37			4.07	3.72
	Y64	3.15		3.55	3.56	3.42
	R100			2.98		2.98
	Y64 + R100		3.07			3.07
	Y64 + R200			2.89		2.89
64	Y4	**				**
	Y16	**				**
	Y64	3.91			6.86	5.39
	Y256				4.66	4.66
	Y64 + R100		3.07			3.07
128	Y64 + R100		3.19			3.19
256	Y256				9.24	9.24
	Y1024				5.00***	5.00***

* See Table 3.
** Unable to pupate.
*** Film was formed on water surface, larval mortality was very high.



Figs. 12-14. Median larval period of *Aedes aegypti* at each density level. Points for the same amount of yeast per cup are connected by lines. 12. Experiment I. 13. Experiment II. 14. Experiment IV. Figure shown indicates the units of yeast per cup. O : males; ● : females.



Figs. 15 & 16. Median larval period of *Aedes aegypti* at each density level. Points for the same amount of yeast per larva are connected by lines. 15. Experiment I. 16. Experiment IV. ○ : males; ● : females.

TABLE 7 - The ratio of larval to pupal period of the females of *Aedes aegypti*(Experiments I - IV).

Density	Food used*	Exp. I	Exp. II	Exp. III	Exp.IV	Mean
1	Y1				4.88	4.88
	Y4	4.60			3.72	4.16
	Y16	3.96				3.96
	Y64	3.17				3.17
	Y64 + R100		2.84			2.84
4	Y4	4.86			8.47	6.62
	Y16	4.17			3.72	3.95
	Y64	3.42				3.42
	Y64 + R100		2.91			2.91
16	Y4	**				**
	Y16	4.06			7.93	6.00
	Y64	4.06		3.80	4.09	3.98
	R100			2.94		2.94
	Y64 + R100		3.02			3.02
	Y64 + R200			2.88		2.88
64	Y4	**				**
	Y16	**				**
	Y64	4.96			**	>4.96
	Y256				5.37	5.37
	Y64 + R100		3.25			3.25
128	Y64 + R100		4.12			4.12
256	Y256				9.75****	9.75****
	Y1024				5.45***	5.45***

* See Table 3.
, * See Table 6.
**** Only three females pupated.

In Fig. 21, the relation between mean wing length and mean thorax length is shown for each density level in Experiment II and for each type of food in Experiment III. In density level of 16 or more in Experiment II, both wing and thorax decrease in length along a straight line with increasing density. However, in densities lower than 16, decreased wing length and rather unchanged thorax length are shown, that is, the points for density levels of 1 and 4 are situated above the line through the points for density 16 to 128. The larvae in lower density receive relatively large amounts of food, because the amount of food per cup was kept constant in this experiment. Therefore, it may be said that at these low density levels the adults resulting from favorable conditions have relatively shorter wing length than those from less favorable conditions.

The same is seen in Experiment III, where different diets were given to the larvae with the same density of 16. The point for the adults from the culture containing yeast 64 units plus rabbit pellets 200 units, which is more suitable than yeast 64 plus rabbit pellets 100 used in Experiment II, is situated above the line through the points for density 16 to 128 in Experiment II, and the point for the less suitable diet, yeast 64, below the line.

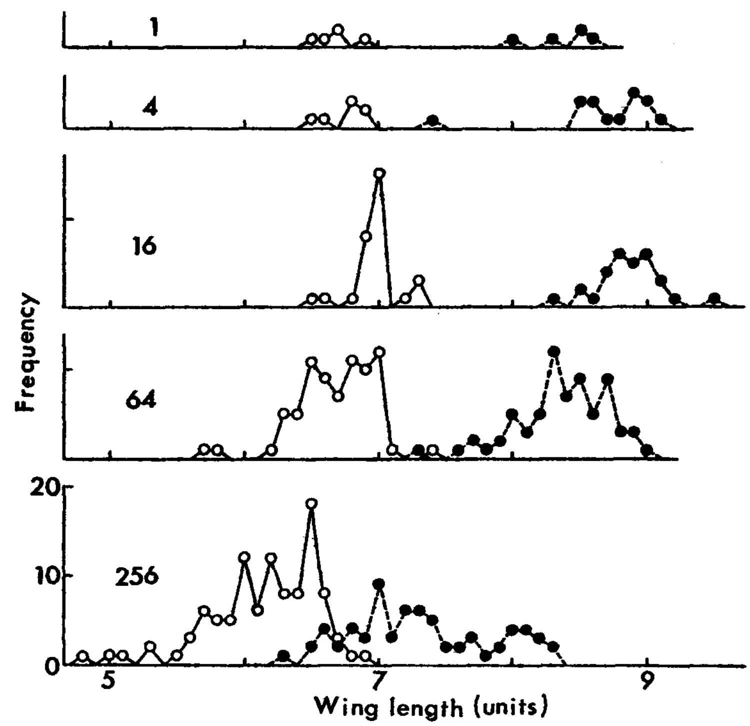


Fig. 17. Frequency distributions of wing length of *Aedes aegypti* (Experiment II). Figure indicates larval density. O : males; ● : females.

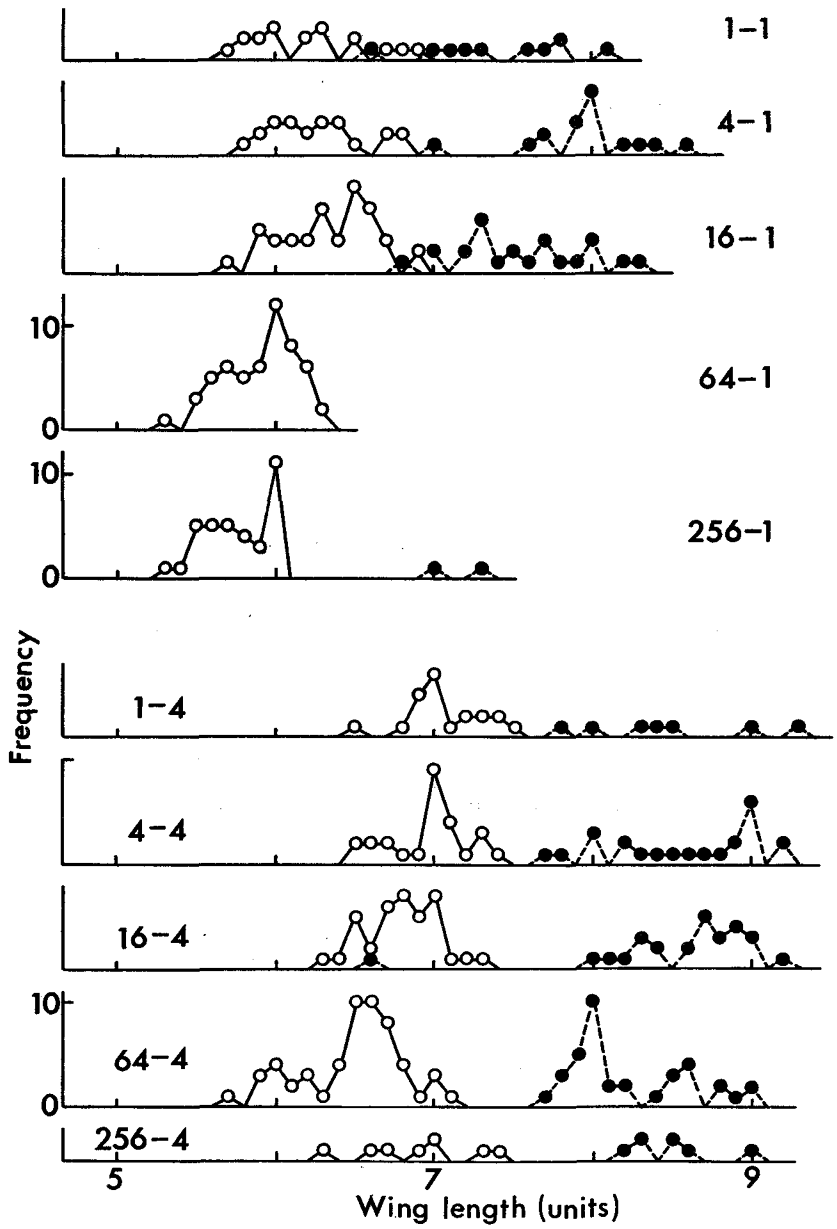


Fig. 18. Frequency distributions of wing length of *Aedes aegypti* (Experiment IV). 16-4, for example, indicates that the larval density is 16 and the amount of yeast is 4 units per larva. ○ : males; ● : females.

In Experiment IV, the situation becomes more complicated, because the experiment consisted of two series of constant amount of food per larva, and it is not easy to say which combination of larval density and amount of food is more favorable for the larval stage, especially at lower density levels. However, it is seen that the relative wing length to thorax length for larger amounts of food or lower density of larvae tends to be smaller than others.

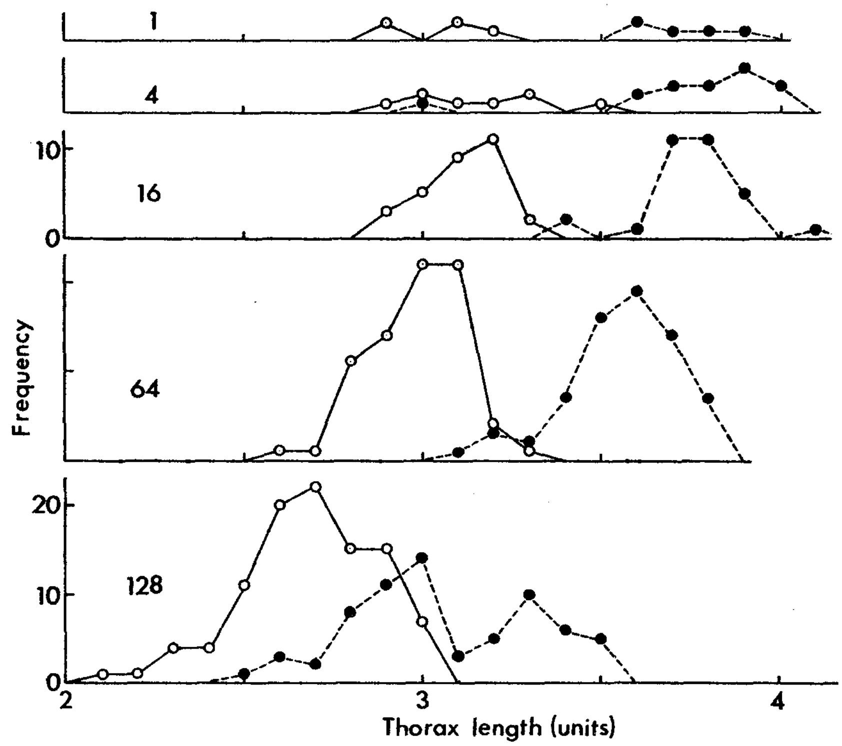


Fig. 19. Frequency distributions of thorax length of *Aedes aegypti* (Experiment II). Figure shown indicates larval density. O : males; ● : females.

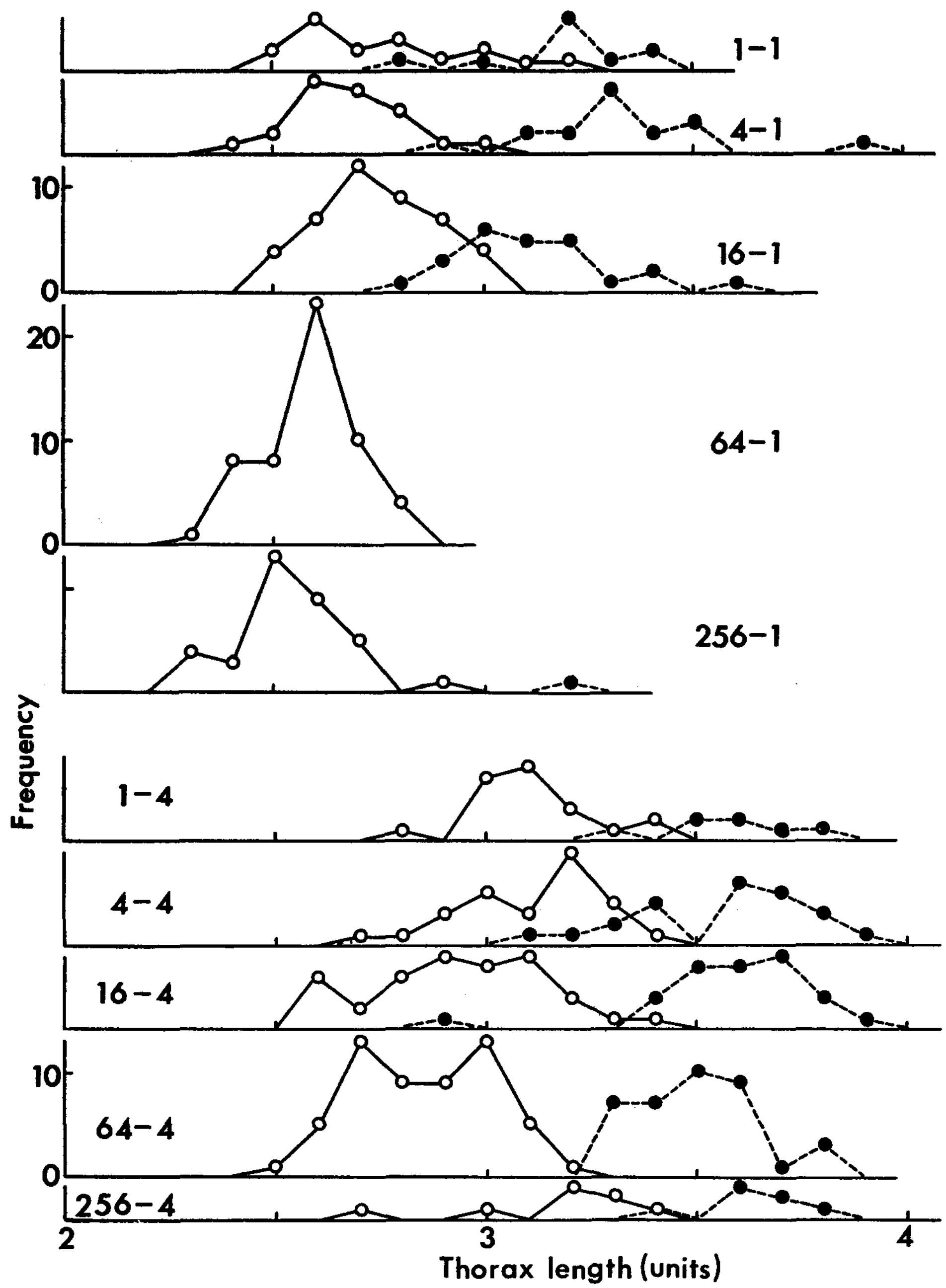
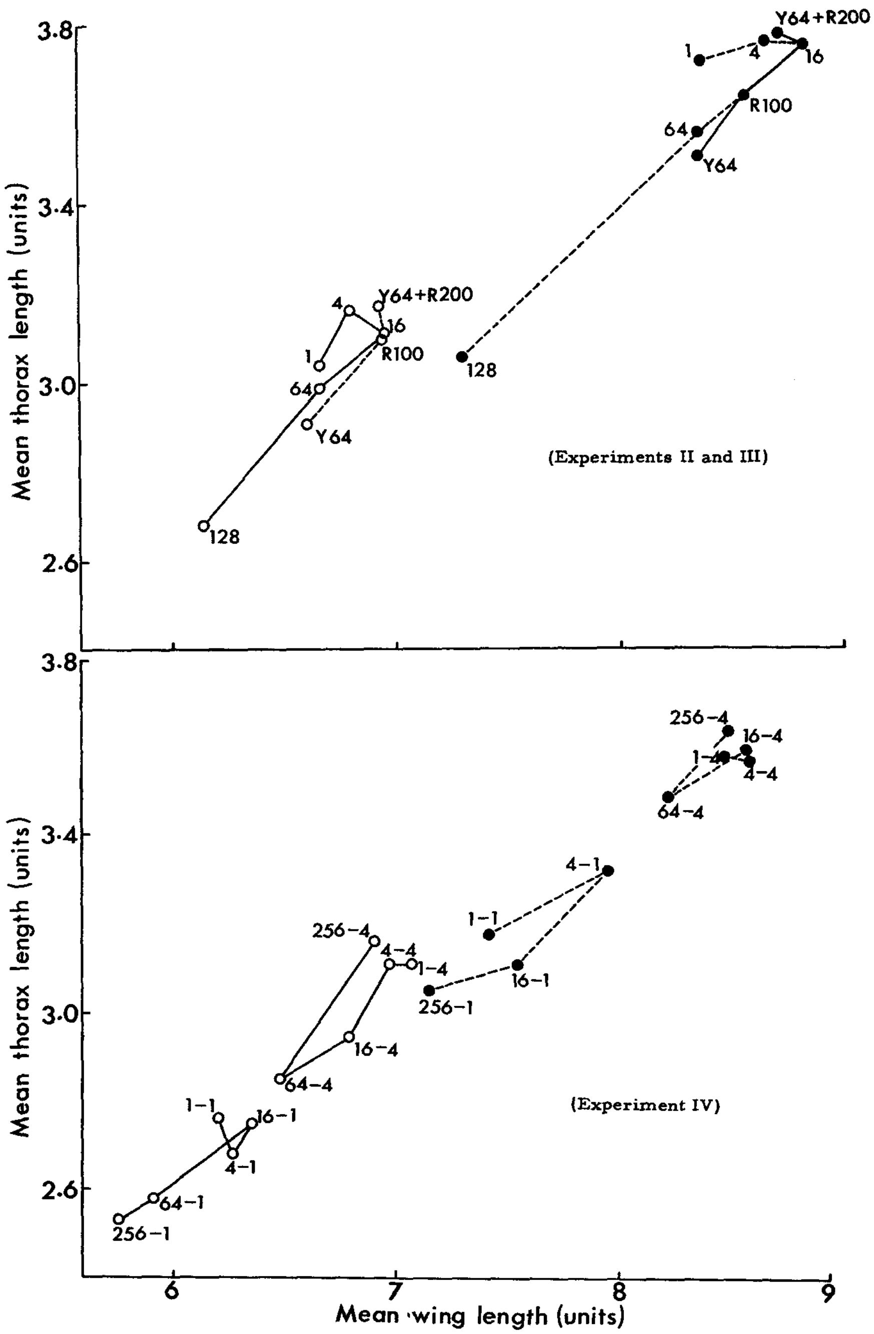


Fig. 20. Frequency distributions of thorax length of *Aedes aegypti* (Experiment IV). 16-4, for example, indicates that the larval density is 16 and the amount of yeast is 4 units per larva. O : males; ● : females.



Figs. 21 & 22. The relation between mean thorax length and mean wing length of *Aedes aegypti*. Figure shown indicates larval density in Experiment II, ~~and~~ and Y, R, and accompanied figure indicate yeast, rabbit pellets, and their amounts in units in Experiment III. In Experiment IV, 16–4 for example, indicates larval density – yeast units. O : males; ● : females.

The adults from the culture with density 1 and yeast 4 per cup are not considered to have a relatively smaller wing length than other densities, unlike Experiment II. This is perhaps because of the fact that the food of yeast 4 in Experiment IV is apparently less favorable than that of yeast 64 plus rabbit pellets 100. The adults with relatively small wing length from low larval density seem to appear only when the amount of food is large.

CONCLUSIONS

The results obtained are summarized in Table 8. The density in this table is used in a relative sense to food quantity. Actual density differs according to the amount of food.

TABLE 8 - Summary of the effects of larval density in *Aedes aegypti*.

Density	Larval mort.	Larval period	Variation in larval period	Sex ratio	Wing length	Thorax length	Wing/ thorax
Very low	Low	Short	Small	1/1	Large	Large	Small
Low	Very low	Very short	Small	1/1	Very Large	Large	Large
High	High	Long	Large	♂ > ♀	Small	Small	Large

High larval density apparently has detrimental effects on the mosquito. Interesting is the relation between very low and low densities. The characteristics seem to indicate that the adults from very low larval density have a slightly reduced flight ability in comparison with those from less low density, as far as judged from the relative wing length. However, repeated experiments are desired, as the number of mosquitoes used in lower densities was not very large.

CONSIDERATIONS ON THE MANNER IN WHICH LARVAL DENSITY PRODUCES ITS EFFECTS

From the preceding sections, the effect of larval density is apparent, but its process was not particularly investigated. Since no effects of metabolic wastes of larvae have been demonstrated (Bar-Zeev, 1957; Shannon and Putnam, 1934), high larval density seems to influence the mosquitoes through the stimulation of increased mutual contacts.

Shannon and Putnam (1934) stated "DeBuck, Schoute, and Swellengrebel (1932) claim ... that when they (anopheline larvae) live in overcrowded conditions food may remain undigested in the alimentary tract from 12 to 24 hours ... Improper nourishment due to massing habits of the larvae (of *Aedes aegypti*) may account for this (phenomenon at high larval density) ...". However, the situation seems to be more complex than Shannon and Putnam (1934) thought, and neuro-physiological processes may be involved.

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