# INHERITANCE OF THE LENGTH OF LIFE IN DROSOPHILA AMPELOPHILA.

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## 1. INTRODUCTION.

I have been experimenting with two different strains of the fruit fly that differ to a marked degree with respect to the length of life. The first or Inbred stock lives an average of about 37 days. The second or Truncate stock lives an average of about 21 days. In both stocks the average life of the male is somewhat longer than that of the female. It is the purpose of this paper to show the behavior of the shortened length of life of the Truncates in heredity. The evidence bears especially on the behavior of the  $F_1$  and  $F_2$  generations that result from crossing the Inbred and Truncate stocks. I shall also present evidence that bears on the question as to whether or not any relation exists between the length of life and the number of offspring produced by these flies.

The data upon which this paper is based grew out of a study of fertility and sterility in these strains. It was found necessary in connection with these studies to keep a careful record of the length of life of the parents. This paper is an analysis of that record. The data includes the record of \$98 individuals that were bred in pairs from September, 1911, to April 1913.

The flies were in all cases used as the parents of the next generation and consequently bred in pairs. Accordingly a male and a female were in each case exposed to exactly the same environmental conditions. It is not to be overlooked that the flies live for several weeks, and since the pairs were constantly being made up the environmental influences would be practically constant. I made it a rule to transfer these flies to new bottles every ten days. It is necessary to transfer the parents more frequently in very warm weather, since offspring will hatch which cannot be distinguished from the parents.<sup>\*</sup> As a matter of fact it is safe to say that in

<sup>\*</sup> I have had *Drosophila ampelophila* to complete development from the egg to a fully formed fly within seven days at Woods Hole, Mass.. in July, 1913.

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these experiments not more than 15 per cent. of the transfers were made before the tenth day. A census was taken of the parents practically every day. In a few cases five days may have elapsed before a record was entered. In case a fly was dead the sex was noted and recorded.

This record, then, includes the length of life of the relatively long-lived Inbred stock; the short-lived Truncate stock; the hybrid offspring between the two stocks and the life of the grandchildren.

## 2. ANALYSIS OF THE DATA.

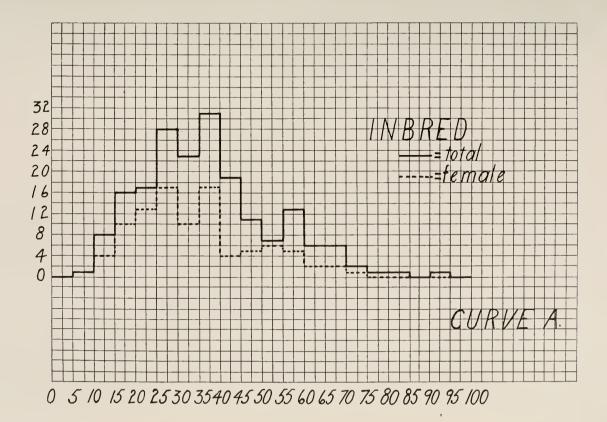
The curves which follow are plotted from the life records of S98 flies which are recorded in Part 1 and Part II of my Studies on "Fertility and Sterility in *Drosophila ampelophila*."\* The length of life is expressed in days and is indicated by the abscissa, while the number of individuals is in each case expressed by the ordinate.

Curve A shows the distribution of the mortality of the Inbred stock. The curve is drawn from the records of 191 individuals. The average life of this lot is 37.4 days. The 94 males lived an average of 40.5 days; 97 females lived an average of 34.5 days. The males lived six days longer than the females.

Curve B shows the distribution of mortality of the 272 Truncates, the average life of which was 21.4 days. The 96 males averaged 26.9 days; the 176 females 18.5 days. The males of this stock lived 8.4 days longer than the females. It is to be noted that the flies of this stock live approximately half as long as those of the Inbred stock.

The hybrid that results from crossing the Truncate and Inbred stocks lives longer than either parent, as is brought out in curve  $C^9$ . For, while the parents live 21.4 and 37.4, respectively, the offspring from the cross live 47 days. This record is based on 42 flies. Thirteen males lived 47.8 days, while 29 females lived 46.4 days. The data is too small to base any safe conclusion in regard to any difference that may exist in the length of life between the male and the female. That the hybrid lives longer than either parent is also borne out by curve C, where a partial record is given of 218 flies. The experiment was discontinued after thirty days, at the end of which time it was found that only 19 per cent, of the flies had died. The mortality in this case corresponds fairly well with the mortality in the case as shown in the curve  $C^4$ , in which seven in 42 died within the first thirty days, a mortality of 17 per cent.

<sup>\*</sup>Journal of Experimental Zoology, 1914. Vol. XVII, Nos. 1 and 2.

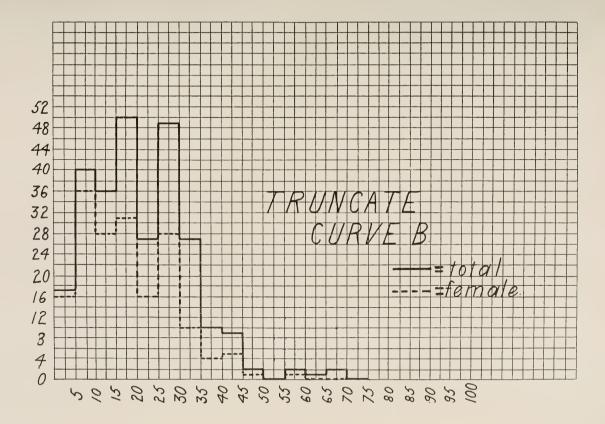


A study of curves D and E shows that the shortened length of life of the Truncates reappears again, and this is true whether the grandchildren have descended from the Truncate male or Truncate female. The 128 flies descended from the Truncate grandmother lived an average of 29.5 days. The 66 males lived 32.8 days, while 62 females lived 25.9 days. The 89 flies that descended from the Truncate grandfather lived an average of 29.3 days. There were 45 males which lived 31.1 days, while 44 females lived 27.3 days.

### 3. Discussion.

The foregoing data brings out the fact that when the Truncate stock with an average life of 21.4 is crossed to the Inbred stock with an average life of 37.4 days, the hybrid that results lives 47 days. If the complex of factors or whatever concerned upon which the length of life in these flies depends, behaves anything like Mendelian characters in the sense that segregation and recombination takes place, then we should expect the shortened length of life of the Truncates to reappear among the grandchildren. A study of the curves verifies the expectation, for the grandchildren live an average of only 29.5 days.

A study of the curves will show in each case three modes which correspond with three periods of the greatest mortality. The meaning of such a phenomenon is obscure, and had the experiment not extended over a long period of time I would be inclined to doubt its reality. There is a possibility, however, that these depression periods correspond with the output of the sex products. My experience in isolating eggs day by day laid by over 200 females seems to indicate that the eggs are laid in cycles that is. a female begins to lay eggs when two or three days old. Her egg production gradually rises to a maximum, and then it declines almost to zero. In fact she may cease to lay eggs for a day or two and then a new cycle begins which runs the same course, and this in turn is followed by a third. In the period when the female ceases to lay eggs she is most likely to die. However, if a female survives such a period at the close of the third cycle she will as a rule live to a ripe old age, depositing a few eggs occasionally. It is barely possible that these mortality periods correspond to the depression periods in the egg-laying cycles. It must be admitted however, that critical evidence is hard to obtain, since the egg production seems to be influenced by several factors. Moreover it is not evident that such an explanation applies to the male.



#### 4. LENGTH OF LIFE AND PRODUCTIVITY.

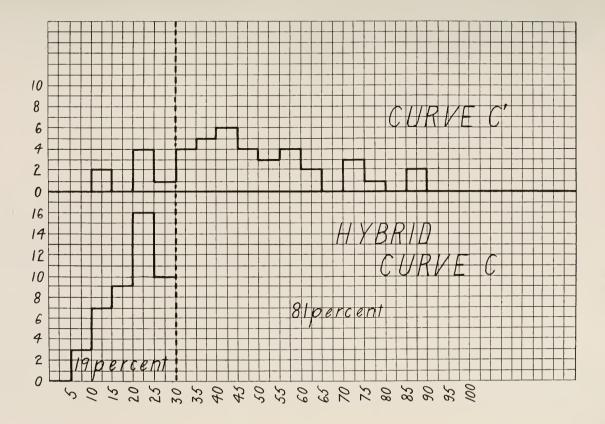
I shall here analyze the data with respect to the productivity of these stocks as determined by breeding in pairs. It is obvious that if a female that would give rise to a large number of offspring should for some reason meet premature death, there would be a correlation between the length of life and the number of offspring produced. The problem, however, is more complicated. In the case of the Truncates it is not evident just how much such a factor as the shortened length of life enters into the results, for I have been able to show that this stock is deficient not only in egg production, but also that marked incompatibility exists between egg and sperm.

In the following curves, F, G, H, I, evidence is brought together that shows the productivity of the F. Truncates. G. The Inbred. H. The Hybrid that results from crossing F and G; and I. The  $F_2$  generation that results from crossing F and G.

In these curves vertical distances express the number of pairs, while horizontal distances express the number of offspring produced. A glance at Curve II, which gives the productivity of the hybrids when the individuals expressed by curves F and G are crossed, moves decidedly to the right. This is evident despite the fact that the experiment was discontinued at the end of thirty days. Curve 1 expresss the output of the  $F_2$  generation. It is evident that the low production of the Truncates reappears among the grandchildren.

This evidence goes to show that the complex upon which productivity depends is inherited in the sense that low productivity skips a generation when crossed into a high producing strain. In fact the productivity of the hybrid fly is greater than the productivity of both parents combined. I have demonstrated in previous studies that the increased productivity on the part of the hybrid is not due in this case to the increased fertilizing power of the gametes beyond that of the highest producing stock, but is due to a greatly increased output of eggs.

As a matter of fact the fertilizing power of the gametes of the hybrid (*inter sc*) is lower than the fertilizing power of the gametes of the highproducing parent. It is evident that the low productivity of the Truncate reappears in the  $F_2$  generation and that this holds true in both the eross and its reciprocal.



## 5. GENERAL DISCUSSION.

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The following is offered by way of explanation of the foregoing facts. Let it be assumed that the complex upon which the length of life of the wild fly depends is expressed by the formula AB. The Truncate stock arose as a mutation from the wild stock and possibly some factor has changed to a. Consequently its formula would be aB. The inbred stock had been in captivity for some time, and it is possible that the B had changed to b. Its formula would be Ab. On crossing these two stocks a hybrid would result, the formula for which is abAB. Consequently in the hybrid, normal conditions are restored, and a fly results that lives longer than either parent. The same explanation holds in the case of the increased egg production to be seen in the hybrid. If this is true we should expect to find wild stocks that live about fifty days and with high egg production and high fertilizing power of the gametes combined. They should be very high producers. The number of factors, however, is not looked upon to be as simple as the formula would seem to indicate. Instead of two factors as the formula shows, there may be many hundreds, but the principle is the same. The things lost or changed in the germ plasm of one stock are compensated in the hybrid by the factors transmitted by the other stock, and thus normal conditions are restored.

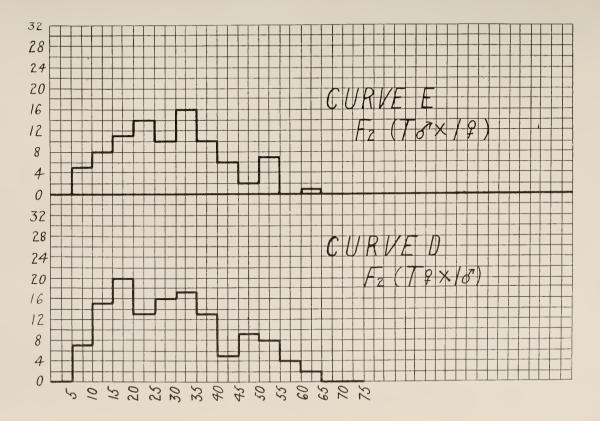
### 6. Conclusions.

1. Hybrids between the Truncate stock and the Inbred stock are more vigorous than either parent as shown by the fact that the hybrid lives 47 days while the parents live 21.4 and 37.4 days respectively.

2. The flies from the Truncate stock live 21.4 days. The females live 18.4 while the males live 26.4 days.

3. The flies from the Inbred stock live 37.4 days. The females live 34.5 days while the males live 40.5 days.

4. The shortened length of life of the Truncate stock reappears among the grandchildren after skipping a generation when crossed to the Inbred stock. The grandchildren lived an average of 29.5 days. Those descended from the Truncate grandmother lived 29.5 days. The males lived 32.8 days and the females lived 25.9 days. The files descended from the Truncate grandfather lived 29.3 days. The males lived 31.1 days, while the females lived 27.3 days.



5. It seems not improbable that the length of life and the coming to maturity of the germ cells may be in some way physiologically connected.

6. The low productivity of the Truncate skips a generation when crossed to a high-producing strain and reappears in the  $F_2$  generation. It is difficult to correlate the length of life in these strains with the number of offspring produced, because it is evident from my other studies that the fertilizing power of the gametes as well as egg production are involved as variable factors in productivity.

