Letters to the Editor.

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Starvation Life Curves.

FOR some years past I have been occupied with the experimental study of duration of life. Nine papers dealing with the subject have appeared in the *American Naturalist* (vols. 55-58). The particular suitability of *Drosophila melanogaster* for the experimental study of this problem arises chiefly from three considerations: (1) The duration of life of this fly in *days* is very nearly the same as that of man in *years*, and the form of the life curve over the biologically equivalent life span is almost precisely identical in the two forms; (2) Drosophila can be easily and successfully grown under controlled laboratory conditions, by means of a technique in many respects the same as that used in the cultivation of bacteria; (3) the genetics of Drosophila have been more completely worked out, thanks to Morgan and his collaborators, than in the case for any other organism whatever.

Normally the living organism gains its energy for the conduct of life, and material for the repair, within limits, of the wastage of its tissues in the business of living, by the process of taking food. In other words, the regular re-winding of the vital clock is accomplished by feeding. If this renewal of the re-winding process is defective in any particular, the result will be to shorten life below what would have been attained under more perfect metabolic functioning. But always when we study duration of life under normal conditions, we are dealing with the combined effects of two variable complexes—inborn organisation, on one hand, and environment, including renewal of available energy and substance by food, on the other. Suppose, now, we eliminate the effect of as much as possible of the second complex experimentally. We shall then be in a better position to estimate how much of the normal variation in duration of life observed among different individuals is due to differences in their inborn make-up, their physico-chemical organisation.

How can this be done experimentally? Clearly by doing two things: (*a*) preventing completely access to food of any sort; (*b*) keeping temperature, moisture, and as many other variables of the physical environment as possible, constant throughout life. Such differences amongst individuals in respect of duration of life as then appear will be almost wholly due to innate protoplasmic, structural, constitutional differences, since the small residue of uncontrolled environmental variables will be unimportant ones, trivial in their effect upon the organism. The form of the life curve so obtained will be in a sense that which is basic to the species or variety. The idea of controlling the food factor of the environmental complex by starvation is methodologically of importance. It is extremely difficult to ensure experimentally that two different animals get identical food, quantitatively and qualitatively. But, with some care, it is easy to see that neither gets any food at all. In short, by complete starvation, we can make constant the most difficult of all environmental variables to control accurately in an experiment.

These considerations suggest that such starvation life curves may furnish a powerful analytical tool for the more penetrating study of the biology of life duration. Consider specifically the case of Drosophila. We have shown in this laboratory (*American Naturalist*, vol. 56, p. 174; vol. 57, p. 153; vol. 57, p. 289) that certain genetic constitutions are invariably associated with certain definite forms of life curves. Wild type Drosophila has a characteristic life curve with a definite absolute mean duration of life and with a characteristic shape. These attributes of the life curve are constant under constant environmental conditions. Under the same environmental conditions, flies which carry the gene for the recessive wing character *vestigial*, whether alone or pure, or in combination with other mutant genes, exhibit life curves which differ widely in every important respect from the curves which describe the duration of life of wild type flies. They have a much shorter absolute duration of life than the wild type, and the shape of the life curve when put upon a comparable basis by measuring age in centiles of the equivalent life span (*cf.* Pearl, *American Naturalist*, vol. 56, p. 398) is widely different from that for wild type flies. All this is clear. But do these differences depend upon (*a*) differences in the inborn physico-chemical organisation, solely and *per se*, of the two sorts of flies, or upon (*b*) differences in the effective reactions of these two kinds of flies to the *same* environment, including most particularly food? Or to put the experimental question, will wild type and vestigial strains of Drosophila show the same kind of differences in their life curves when these curves are determined under conditions of complete starvation, that they do when both sorts of flies are fed the same kind of food?

A rather elaborate and precise technique was worked out to ensure complete absence of food from the moment of emergence as imagos. Observations were taken every six hours until the last fly had died. The duration of life of 3632 individual flies under complete starvation was recorded.

The net result was that under complete starvation the mean duration of life and the form of the life curve *are almost identically the same* in vestigial as in normal wild type flies, though under conditions of full feeding the wild type flies live roughly three times as long as the vestigials. Actually the vestigials have a slightly *longer* mean duration of life under starvation than the wild type flies. This fact would seem to be of considerable importance from the point of view of genetics. It is a specific example of the general principle that the somatic expression of any genetic factor in any particular case is in part a function of the general environmental level which prevails in that case. It has been demonstrated, as already stated, that *under the standard feeding conditions for laboratory bred Drosophila* the gene for vestigial has as a part of its somatic expression a very considerably reduced duration of life as compared with the wild type. There are few cleaner-cut cases of Mendelian segregation to be found in the whole literature of genetics than that upon which the above statement is made. Yet the present study shows that the whole of that part of the somatic expression of the vestigial gene which is differential in respect of duration of life disappears under another system of "feeding" wild type and vestigial flies (namely, complete starvation). This fact does not in the least invalidate the earlier results cited on the inheritance of duration of life. Those results are *facts* just as much as the present observations. It merely emphasises once more, in a rather striking way, the extraordinary caution which is always necessary in interpreting the results of genetic experiments. It also, of course, points the way to new and very promising lines of further experimental attack upon the problem of duration of life.

The complete account of these experiments is in press, to appear shortly in the *American Naturalist*.

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