Experimental Studies on the Duration of Life. IV. Data on the Influence of Density of Population on Duration of Life in Drosophila
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EXPERIMENTAL STUDIES ON THE DURATION OF LIFE. IV. DATA ON THE INFLUENCE OF DENSITY OF POPULATION ON DURATION OF LIFE IN DROSOPHILA[1]

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I

FAIRLY early in our experimental work on duration of life in *Drosophila* it became apparent to us that the number of flies per bottle, or, since the bottles used are of uniform size, the density of population, had some influence on the mean duration of life of the flies, when other environmental conditions are constant. Such a relationship might reasonably be expected *a priori,* from what is known of the influence of this factor on human death rates, commonly expressed as Farr's Law (*cf.* Farr, W. (35), Brownlee, J. (36, 37)), and on other biological functions, such as growth (Semper, K. (38), Bilski, F. (39)), resistance to poisons (Drzwina and Bohn (40)), rate of reproduction (Pearl and Surface (41), Pearl and Parker (42)), etc. As soon as it was recognized that this variable, density of population, might influence our experimental results with *Drosophila,* care was taken in setting up experiments to make this a constant in each case. At the same time the records of the earlier work were carefully re-examined to determine what part this variable may have played in the results. Happily it was found that in none of our work so far published upon the duration of life in *Drosophila* had density of population varied enough to have any appreciable effect upon the results or conclusions.

As was recently pointed out by Pearl and Parker (42), however, "there can be no question that this whole matter of influence of density of population, in all senses, upon biological phenomena, deserves a great deal more

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investigation than it has had. The indications all are that it is the most important and significant element in the biological, as distinguished from the physical, environment of organisms." In pursuance of this idea we desire to present in this paper our accumulated *statistical* data on the influence of density of population upon duration of life in *Drosophila*. This material is to be regarded as preliminary rather than final. For reasons which will appear as we proceed, we are inclined to withhold final conclusions as to the exact form of the regression of duration of life upon density until we have completed an extensive *ad hoc* experimental investigation of the problem. This experimental work is now in progress and we hope to be able to report upon it in full in the course of the next year. In the meantime we have an impressive body of statistical data gathered from the control groups of other experiments which it seems desirable to discuss now in a preliminary way.

II

The data of this study are derived from the normal control groups of various experiments on duration of life which we have carried out with *Drosophila*, according to the technique described by Pearl and Parker (27). All of the determinations of duration of life recorded in the tables of this paper were made under constant conditions of temperature (25° C.), food, etc., as described in the paper referred to. We have divided the material for the purposes of the present study into three groups by stocks (*cf.* Pearl and Parker (27)), *viz.:* (*a*) wild type flies, including our Old Falmouth, New Falmouth, and Eagle Point stocks, (*b*) Sepia, and (*c*) Quintuple.

Throughout this paper density of population is taken as the *initial density* (number of flies per bottle) in the small bottles used in testing duration of life. Thus a density of 22 means that 22 flies started in this particular bottle. As time went on the number was diminished by deaths until finally none was left. One of course might use as the variable mean density over the whole life of a bottle, but a little thought will show that this would be an erroneous procedure when one is dealing with duration of life as the second variable, because *mean* density bears a direct and implicit functional relation to mean duration of life of the flies in the bottle. We shall be on a clearer footing to take *initial* density as the variable. Since the cubical content of the bottles is constant throughout, there is no necessity of reckoning density per c.c. The number of flies per bottle can be taken as the measure of density, and a good deal of useless computation saved.

We are indebted to Dr. John Rice Miner for aid in the computations.

III

Table I presents the data for the correlation of duration of life with density of population for the wild type flies. The material is in the usual form of a correlation table.

An examination of this surface suggests at once that the regression is probably non-linear. Owing to the manner in which the material was obtained (by compilation of the control series of a number of different experiments) it results that the different arrays have rather highly different total frequencies. The number of flies per bottle was in no way artificially selected or predetermined in this material. Instead it was determined solely by the aggregate fertility of the mating bottles furnishing the material for each particular experiment. As has been explained in the first of these Studies (Pearl and Parker (27)), the routine procedure in our experiments is to put into one bottle for duration of life test all the flies emerging as imagoes at the same time (*i.e.*, usually on the same day). It therefore would result that if the hatch was particularly good on some day, there might be as many as 90 flies in the duration of life bottle initially. On the other hand, there might be only 2 flies, because only that number emerged on that particular day.

Even in spite of the differences in the frequencies of

TABLE I

CORRELATION SURFACE FOR THE VARIABLES (*a*) DURATION OF LIFE, AND (*b*) INITIAL DENSITY OF POPULATION. WILD STOCKS OF DROSOPHILA

Age at Death	Number of Flies in Bottle																							
	1–	5–	9–	13–	17–	21–	25–	29–	33–	37–	41–	45–	49–	53–	57–	61–	65–	69–	73–	77–	81–	85–	89–	93–	Total
1–......	15	41	35	29	35	45	37	3	27	4	10	28	20	....	12	19	....	12	....	....	....	2	....	16	390
7–......	38	49	47	48	39	38	30	20	22	6	6	8	24	4	13	11	1	17	13	2	....	....	....	43	479
13–......	24	55	44	45	59	35	39	20	28	3	3	12	14	23	14	19	1	8	10	5	1	2	....	20	484
19–......	19	53	57	30	64	37	38	33	24	17	51	30	32	14	17	33	7	5	46	13	10	22	....	47	699
25–......	31	75	59	45	70	42	79	21	31	22	20	20	32	7	17	20	15	7	40	3	15	21	....	5	697
31–......	19	87	88	55	76	90	78	47	44	10	47	31	33	5	13	68	11	23	50	13	16	52	....	4	960
37–......	14	72	108	84	118	94	80	77	45	19	31	36	60	3	38	70	16	4	20	11	14	27	....	8	1,049
43–......	21	73	126	86	161	83	80	39	53	16	32	66	67	....	23	18	46	32	33	5	17	2	....	19	1,098
49–......	19	84	110	109	120	124	117	43	71	20	44	71	70	....	14	35	23	33	7	11	7	12	....	2	1,146
55–......	10	75	85	102	102	71	109	47	37	38	56	35	37	....	15	38	6	16	1	4	....	17	....	9	910
61–......	5	38	61	96	97	55	70	50	39	35	42	55	49	....	11	16	3	18	2	11	1	7	....	13	774
67–......	1	25	36	54	66	41	75	19	13	17	18	44	31	....	11	7	3	3	....	1	1	5	....	....	471
73–......	....	9	11	33	33	34	30	19	8	13	13	13	15	....	21	9	1	15	....	1	....	....	....	....	278
79–......	....	5	4	20	17	13	16	10	4	5	4	10	11	....	2	6	....	6	....	....	....	....	....	....	133
85–......	1	2	6	8	3	8	9	5	3	....	2	2	2	....	6	3	....	4	....	....	....	....	....	....	64
91–......	....	....	....	3	....	....	5	3	2	1	1	2	1	....	5	....	....	5	....	....	....	....	....	....	28
97–......	....	....	....	....	....	1	....	....	....	....	....	....	....	....	1	2	....	1	....	....	....	....	....	....	5
103–......	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	1
109–......	....	....	....	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	1
Total....	217	743	877	847	1,060	812	892	456	451	226	380	463	498	56	234	374	133	209	222	80	82	169	....	186	9,667

the several arrays, it still seems probable from mere inspection of the general surface that the regression is non-linear. This idea is strengthened by examination of the regression line itself, shown in Fig. 1.

FIG. 1. Mean duration of life of *Drosophila* for different initial densities of population. Wild stocks.

It is seen from this diagram that, neglecting the great dip of the line at density 55 which is consequent upon a very small array with large probable error, the general sweep of the curve indicates an optimum density (greatest mean duration of life) in the general region of 35 to 45 flies per bottle, with a decline on either side of that point, but falling lower on the side of high densities than on that of low.

From this table we have the following constants:

$$r = -.0511 \pm .0068,$$
$$\eta = \quad .2443 \pm .0064.$$

There can be no question that the regression is non-linear. Blakeman's (43) criterion has the following value:

$$\zeta = \quad .0571 \pm .0031.$$

It must therefore be concluded that the regression is significantly skew.

The correlation between duration of life and density of population in the case of the Sepia stock is shown in Table II.

TABLE II

CORRELATION SURFACE FOR THE VARIABLES (*a*) DURATION OF LIFE, AND (*b*) INITIAL DENSITY OF POPULATION. SEPIA STOCK

Age at Death	Number of Flies in Bottle																					
	1–	5–	9–	13–	17–	21–	25–	29–	33–	37–	41–	45–	49–	53–	57–	61–	65–	69–	73–	77–	81–	Total
1–	7	29	27	23	13	15	....	1	1	....	2	....	....	....	....	....	....	....	4	1	37	160
7–	10	18	27	27	11	27	2	16	....	5	3	....	....	....	4	....	....	....	3	9	6	168
13–	5	21	23	23	6	33	12	18	1	8	4	....	....	....	8	....	....	....	5	46	1	214
19–	16	27	8	35	9	21	12	21	9	35	8	6	10	....	6	....	....	....	21	17	2	263
25–	7	34	5	20	8	30	17	21	14	26	9	30	15	....	18	....	....	....	38	2	7	301
31–	13	28	40	20	9	20	9	13	8	24	22	4	13	....	14	....	....	....	41	....	....	278
37–	4	28	30	40	15	33	15	7	1	15	11	4	3	....	6	....	....	....	8	2	2	224
43–	9	26	38	35	23	37	12	13	1	24	30	1	1	....	2	....	....	....	27	....	15	294
49–	10	27	36	24	17	19	1	6	....	9	16	1	4	....	1	....	....	....	3	....	11	185
55–	5	18	16	17	19	18	....	2	....	2	8	....	1	....	1	....	....	....	1	....	....	108
61–	3	2	15	10	9	6	1	6	....	3	7	....	4	....	....	....	....	....	1	....	....	67
67–	....	9	6	4	5	3	....	1	....	....	7	....	....	....	....	....	....	....	....	....	....	35
73–	....	....	2	2	2	1	....	....	....	1	2	....	....	....	....	....	....	....	....	....	....	10
79–	1	....	....	2	....	1	....	....	....	....	2	....	....	....	....	....	....	....	....	....	....	6
Total	90	267	273	282	146	264	81	125	35	152	131	46	51	....	60	....	....	....	152	77	81	2,313

Here again there are a number of small arrays and gaps towards the right-hand side of the table, due as before to the method by which the material was got.

The regression of duration of life upon density is shown graphically in Fig. 2.

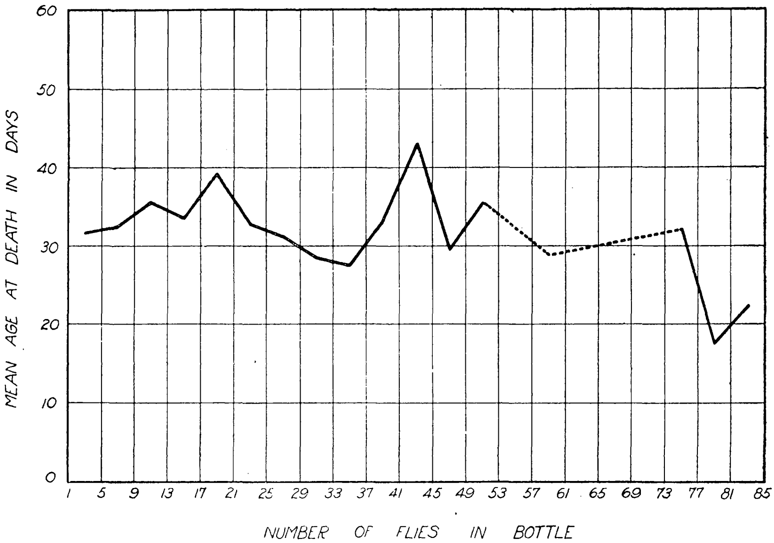

Fig. 2. Mean duration of life of *Drosophila* for different initial densities of population. Sepia stock.

It is apparent from inspection here as before that the regression is not clearly linear, but rather indicates an optimum density in the region of 35 to 45 flies per bottle, with a diminished expectation of life at both lower and higher densities. The constants are

$$r = -.132 \pm .014,$$
$$\eta = .283 \pm .013,$$
$$\zeta = .0629 \pm .0066.$$

The criterion of linearity is nearly 10 times its probable error, and we may therefore conclude for the Sepia stock, as for the wild stocks, that statistically the regression of duration of life upon density of population is significantly skew.

The data for the short-lived Quintuple stock are given in Table III.

Owing to the fact that the Quintuple stock is characterized by low fertility, as well as short duration of life,

TABLE III

CORRELATION SURFACE FOR THE VARIABLES (*a*) DURATION OF LIFE, AND (*b*) INITIAL DENSITY OF POPULATION. QUINTUPLE STOCK

Age at Death	Number of Flies in Bottle														
	1–	5–	9–	13–	17–	21–	25–	29–	33–	37–	41–	45–	49–	53–	Total
1–	22	18	17	15	9	7	15	1	...	...	...	...	...	4	108
4–	21	33	19	31	4	3	9	11	...	...	...	...	...	15	146
7–	26	70	50	50	13	13	20	4	...	...	...	...	...	17	263
10–	22	38	47	28	19	12	10	...	...	...	...	...	...	7	183
13–	15	24	28	29	8	13	12	6	...	...	...	...	...	3	138
16–	8	21	20	19	6	7	4	4	...	...	...	...	...	...	89
19–	11	14	11	12	4	3	1	...	...	...	...	...	...	1	57
22–	5	13	12	4	6	2	1	...	...	...	...	...	...	1	44
25–	2	5	13	7	3	3	2	...	...	...	...	...	...	...	35
28–	...	6	3	3	2	2	1	2	...	...	...	...	...	2	21
31–	...	6	3	1	...	3	1	...	...	...	...	...	...	1	15
34–	2	3	...	3	...	...	...	...	...	...	...	...	...	...	8
37–	1	4	2	...	...	1	...	...	...	...	...	...	...	1	9
40–	1	3	2	...	...	...	2	1	...	...	...	...	...	1	10
43–	3	2	2	...	...	1	...	...	...	...	...	...	...	...	8
46–	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
49–	...	1	1	...	...	...	1	...	...	...	...	...	...	...	3
Total	139	261	230	202	74	70	79	29	...	...	...	...	...	53	1,137

this table is less extensive in either direction than the others.

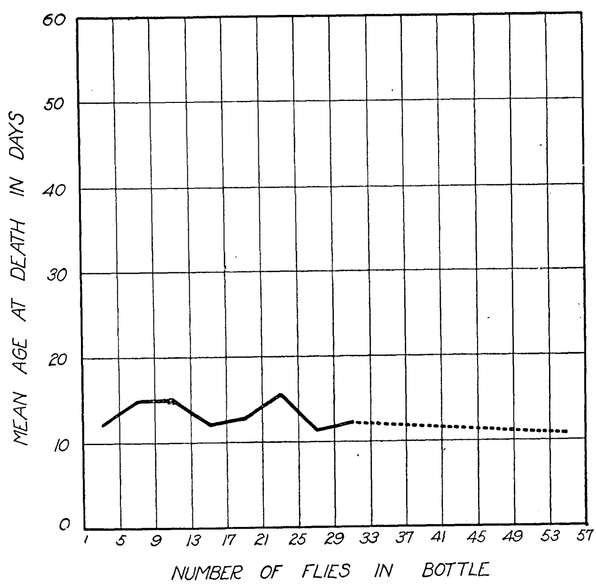

FIG. 3. Mean duration of life of *Drosophila* for different initial densities of population. Quintuple stock.

The observed regression line is shown in Fig. 3.

Here the regression appears at once to be substantially linear, and is proved to be by the analytical constants, which are as follows:

$$r = -.057 \pm .020,$$
$$\eta = .120 \pm .020,$$
$$\zeta = .011 \pm .004.$$

The criterion ζ is less than 3 times its probable error and cannot be regarded as significant.

IV

Putting all the data together, we have here indisputable evidence that the density of population is a significant factor in influencing the duration of life (or death-rate) in *Drosophila*. The correlation ratio η is certainly significant in the case of all three stocks. Its lower value in the case of the Quintuple stock is almost certainly due to the fact that in the Quintuple experience there is not a sufficiently extensive representation of densities. If the other two tables were to be cut off at the density array where the Quintuple is, they also would show a much lower association between the two variables. So, then, the *general portion* of Farr's Law which affirms that death-rate is some function of density of population receives experimental confirmation in a widely different form of life.

When one comes, however, to the precise form discovered by Farr (35) and confirmed by Brownlee (36, 37), the case is not so clear. We do not care to enter upon any detailed discussion of the point now, because we do not care to draw any conclusions as to the true form of the skew regressions observed till we have some additional experimental results in hand. Provisionally, however, it may be said that the indications are that in *Drosophila* something like the following relations hold: (*a*) the lowest density is not the optimum; (*b*) the mean duration of life tends to increase with increasing density up to a certain point which is optimum; (*c*) after the optimum region has been reached, increasing density is associated with diminished duration of life, which presently falls below the lowest figure found with densities below the optimum. These conclusions must for the present be held as tentative.

V

In this paper data as to total duration of imaginal life of 13,117 individuals of *Drosophila* are presented in relation to the density of population. It is definitely shown in the case of Wild, Sepia and Quintuple stocks that there is a significant correlation between these variables. The regression of duration of life upon density appears to be significantly skew in the case of Wild and Sepia stocks. The precise form of the regression and theoretical questions connected therewith are left for discussion in a later paper upon the basis of more extensive material.

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(The plan of numbering citations followed is explained in the second of these Studies.)

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