*EVOLUTION OF FITNESS, V. RATE OF EVOLUTION OF IRRADIATED POPULATIONS OF DROSOPHILA**

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Abstract.—Measurable evolution occurs in laboratory populations of *Drosophila* under strong natural selection. The rate of adaptation to the experimental environment is significantly greater in populations with genetic variability increased by radiation than in the control, nonirradiated populations.

Fisher's[1] fundamental theorem of natural selection states that the rate of increase in fitness of a population at any time is proportional to its genetic variance in fitness at that time. To ascertain the role of genetic variability in evolution one must also know whether an increase in the average fitness of the genotypes of a population leads in general to an increase in the adaptedness of the population to its environment. One of the central questions of evolutionary genetics is whether, as postulated by the Darwinian theory, natural selection can explain the fact that organisms are adapted in their structure and function to the environments in which they live. The experiment reported here tests whether genetic variability induced by high-frequency radiation may increase, with natural selection, the rate of adaptation of a population to its environment.

Experimental Procedure.—Three populations of *Drosophila birchii* are used in the experiment; two of them, 52 and 53, had a previous history of radiation, and the third, 51, was a control.[2] Each population was divided into two subpopulations: 2000 males of one subpopulation were given 2000 r of X rays for each of three generations; the other subpopulation served as control. This radiation procedure, which has been described in detail elsewhere,[3] permits the incorporation of the newly induced with the existing genetic variability. After the third radiation the three experimental populations and their controls were started with 1200 founder flies each. The populations were maintained at 19°C by the serial transfer technique.[4] This technique ensures a rigorous natural selection both among the larvae and among the adults.

Adaptedness to the environment was measured by the average population number ("size") and by the number of flies emerging per week ("productivity"). The experiment was carried out for 116 weeks or about 40 generations.

Results and Discussion.—The population counts, made at approximately two-week intervals, of the irradiated and control populations are represented in Figure 1. Table 1 gives the following parameters with their standard errors: mean population size, regression coefficient of population size on time, mean productivity, and regression coefficient of productivity on time. Time units for the regression are weeks. Mean biomass of the total population, mean biomass produced per week, and their regression on time were also calculated but are not included in the table since they do not differ meaningfully from the parameters given.

The control populations have improved throughout the experimental period both in their population numbers and in their ability to transform the available energy resources into biomass. The size of the control population increases at a

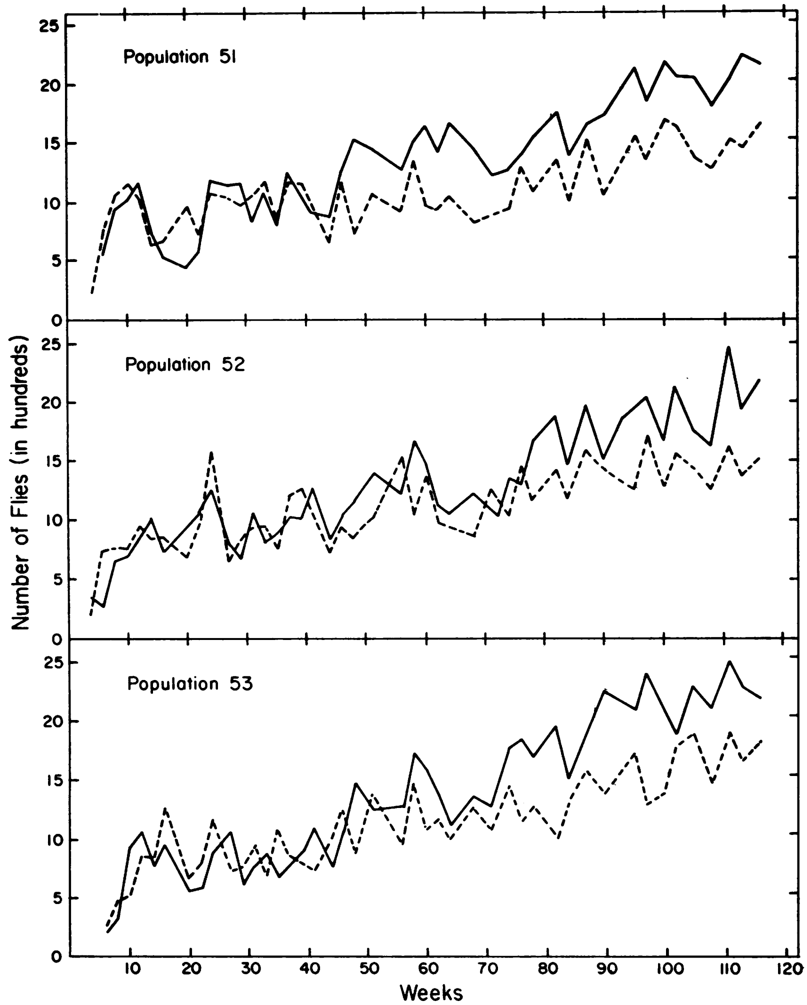

FIG. 1.—Number of flies in six populations of *D. birchii*. *Solid lines*, irradiated populations; *broken lines*, controls.

TABLE 1. *Mean population size, mean weekly productivity, and regression of size and productivity on time of three irradiated populations and their controls.*

	Population Size*		Weekly Productivity†	
	Mean	Regression coefficient‡	Mean	Regression coefficient‡
Control 51	1093 ± 47	6.9 ± 2.0	723 ± 17	2.1 ± 0.7
Experimental 51	1337 ± 73	11.5 ± 3.0	919 ± 23	3.9 ± 0.9
Control 52	1106 ± 53	8.3 ± 2.0	845 ± 18	1.4 ± 0.6
Experimental 52	1283 ± 86	15.2 ± 3.2	937 ± 34	4.1 ± 1.1
Control 53	1121 ± 70	6.4 ± 2.0	822 ± 31	1.4 ± 0.5
Experimental 53	1334 ± 103	12.9 ± 3.2	1004 ± 42	4.7 ± 1.4

* 45 measurements for population size mean and regression.
† 113 measurements for productivity mean and regression.
‡ Time units for the regression are weeks.

rate of about seven flies per week, and their productivity at a rate of nearly two flies per week. After 116 weeks of selection, the populations are about twice as large as at the beginning of the experiment. Natural selection has gradually given origin to new genotypes highly adapted to survive and reproduce under the experimental conditions. Evolution of the adaptedness of populations to their environment under strong natural selection has been observed in laboratory and field studies.[5–8]

The rate of adaptation to the environment is greater in the irradiated populations than in their controls. The size of the experimental populations increases at a rate of about 13 flies per week, and their productivity at a rate of 4 flies per week. The difference between each experimental population and its control was obtained for each measurement throughout the experimental period. The mean of the differences and the regression of the differences on time, given in Table 2, are in all cases significantly greater than zero.

TABLE 2. *Mean difference, and regression of the differences on time, between three populations and their controls.*

	Difference in Population Size		Difference in Productivity	
	Mean	Regression coefficient	Mean	Regression coefficient
Exptl. 51 − control 51	243 ± 36	4.7 ± 1.8	196 ± 12	1.8 ± 0.6
Exptl. 52 − control 52	176 ± 48	6.8 ± 2.0	92 ± 20	2.7 ± 0.9
Exptl. 53 − control 53	214 ± 47	6.6 ± 2.0	182 ± 17	3.3 ± 0.9

Populations with genetic variability increased by hybridization adapt to the environment at a faster rate than parental, genetically less variable populations.[7–10] The superior performance of these populations is likely to be due to the fact that natural selection is more effective in those populations where a greater variety of genotypes are available for selection. The present experiment demonstrates that genetic variability induced by radiation may also result with natural selection in more efficient adaptation of a population to a new environment. (This conclusion, of course, does not apply to man, who has a long generation time and limited reproductive capacity and whose values are contrary to a selective pressure which would eliminate a majority of the population for a considerable number of generations.)

The rate of evolution observed in these populations is considerably higher than the evolutionary rates observed in nature. The increases in population size of about 20 flies and 40 flies per generation in the controls and the experimental populations, respectively, represent an increase of about 2 and 4 per cent of the mean population size per generation. This high rate of evolution is due to strong selection pressure in a constant direction acting on populations with suitable genetic variability. Rapid evolutionary changes have been observed in natural populations of insects adapting to changing environments.[5, 11–12]

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