EVOLUTION OF FITNESS. I. IMPROVEMENT IN THE PRODUCTIVITY AND SIZE OF IRRADIATED POPULATIONS OF *DROSOPHILA SERRATA* AND *DROSOPHILA BIRCHII*[1]

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Received December 15, 1965

HIGH energy radiations speed up the mutation process. Random mutations are expected, on theoretical grounds, to be for the most part deleterious. Unconditionally harmful mutations are, however, eliminated by natural selection more or less rapidly depending on the magnitude of their effect on fitness, so that heavily irradiated populations "recover" rather rapidly almost to the control level of fitness (WALLACE 1951; STONE and WILSON 1957; MOURAD 1962; SANKARANAYANAN 1964, 1965).

Economically beneficial mutants induced by radiation have been selected in barley (GUSTAFSSON 1947, 1952), in the molds *Aspergillus terreus* and Penicillium (HOLLAENDER 1945) and in other forms. In Penicillium, a strain was produced which yields four to five times as much penicillin as that of the original strain. WALLACE (1958, 1963) and CRENSHAW (1965) have shown that mutations induced by radiation may increase the average fitness of otherwise homozygous or nearly homozygous individuals. DOBZHANSKY and SPASSKY (1947) have observed that the fitness of strains homozygous for certain deleterious chromosomes improved when the males were treated with X-rays every generation. The improvement was due to the action of natural selection, since it did not occur in similarly treated lines where selection was not operative.

The present experiments were designed to test whether, with strong natural selection, the increased genetic variability produced by X rays can serve to improve the fitness of experimental populations derived from strains which are not strongly inbred nor completely homozygous.

MATERIALS AND METHODS

Strains of two species *Drosophila serrata* and *D. birchii* were used in the experiment. The Popondetta strain of *D. serrata* had been maintained in the laboratory by mass culture at 19°C for one year before the beginning of the experiment, and at 25°C for the two previous years. The Cairns strain of *D. birchii* had been maintained by mass culture at 19°C for about two years before the beginning of the experiment, and at 25°C for the two previous years. Both strains were derived from impregnated females collected in nature. The *D. serrata* strain was collected by DR. M. WASSERMAN and the *D. birchii* strain by PROFESSOR DOBZHANSKY.

Some 2000 males one to six days old were collected in each species, treated with 2000r of X rays, and then mated to 2000 virgin females of the same age under uncrowded conditions

[1] The work reported here was done under Contract No. AT-(30-1)-3096-6, U.S. Atomic Energy Commission.

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(about 50 pairs of flies per half-pint bottle). From the progeny of each strain, 2000 males and 2000 virgin females were collected, the males treated with 2000r and then mated as before. From the progenies of these new matings, 1200 males and 1200 virgin females of each strain were collected, the males X-irradiated once more with 2000r, and then distributed in two groups of 600, each group being placed in one half-pint bottle with an equal number of females. In this way, two experimental populations of each species were obtained. A control population for each species was established by selecting 1000 males and 1000 virgin females for two generations, and treating them as the experimental populations except for the X-ray treatment. 600 males and 600 females were collected in the third generation and placed in a single bottle to start the control population of each species.

The males of the experimental populations received 2000r in each of the three generations before they were introduced in the bottles to begin the experimental populations. The genome of the males was completely irradiated and had received an average of 4000r. Most of the genome of the females is expected to have received different amounts of radiation, averaging 2000r. The hereditary materials of the first generation of flies born in the populations had received an average of 3000r.

The populations were started at 25°C and maintained by the serial transfer technique. After 51 days, one population was derived from each of the experimental and control populations by taking a sample of 300 adult flies from each and starting with them a new set of populations at 19°C. The 12 populations are described in Table 1.

X-ray treatments were given by MR. DAVID MARSDEN, at the Betatron Department of Columbia University, with a "Superficial Zephyr" machine (Picker X-ray Co.), as follows: Target distance—20.4 cm, Half-value layer—1.9 mm aluminum (1 mm Al filter), 120 kvp, 5 ma, 129.5r per minute. During the treatment the flies were kept in small gelatin capsules (about 200 per capsule) arranged in a single layer.

The serial transfer technique used to maintain the populations has been described by AYALA (1965a). Briefly, the adult flies are introduced in a half-pint milk bottle with a 2 cm layer of SPASSKY's cream of wheat-molasses medium. A double piece of toweling paper, about 5 × 18 cm,

TABLE 1

The 12 experimental populations

Population	Species	Temperature	Origin	Treatment	Initial size	Started
Control 1	*D. serrata*	25°C	Popondetta strain	None	1200	October 1964
Experimental 1	*D. serrata*	25°C	Popondetta strain	Radiated	1200	October 1964
Experimental 2	*D. serrata*	25°C	Popondetta strain	Radiated	1200	October 1964
Control 2	*D. serrata*	19°C	Derived from Control 1	None	300	December 1964
Experimental 3	*D. serrata*	19°C	Derived from Experimental 1	None	300	December 1964
Experimental 4	*D. serrata*	19°C	Derived from Experimental 2	None	300	December 1964
Control 1	*D. birchii*	25°C	Cairns strain	None	1200	October 1964
Experimental 1	*D. birchii*	25°C	Cairns strain	Radiated	1200	October 1964
Experimental 2	*D. birchii*	25°C	Cairns strain	Radiated	1200	October 1964
Control 2	*D. birchii*	19°C	Derived from Control 1	None	300	December 1964
Experimental 3	*D. birchii*	19°C	Derived from Experimental 1	None	300	December 1964
Experimental 4	*D. birchii*	19°C	Derived from Experimental 2	None	300	December 1964

is partially pressed into the medium. No yeast is added. The flies are transferred to a fresh bottle, without etherization, at regular intervals. On Mondays, Wednesdays and Fridays at 25°C, and on Mondays and Fridays at 19°C. When the emergence begins in the bottles where the eggs were deposited, the newly born flies are collected, etherized, and counted, on the same days on which the adult population is transferred to a fresh bottle, and then added to the adult population. The adult ovipositing flies are thus always in a single bottle with fresh food, while a number of bottles for each population contain eggs, larvae, pupae and newly hatched adults. The bottles are discarded on the 28th day at 25°C and on the 38th day at 19°C. Every second week, on Friday, before adding the newly hatched flies, the adult population is etherized, weighed and counted. After being counted, the newborn flies are also weighed on that day in a balance with 0.1 mg sensitivity. Newborn flies are counted individually. The total size of the population is estimated by taking a sample of about 300 flies, which is counted and weighed; the rest of the population is then weighed, and the total number calculated by a simple proportion. When the total population is no greater than about 500, the flies are counted individually. Counts and weighings of all the populations are always done on the same days and in the same order.

D. serrata and *D. birchii* are highly sensitive to ether. The etherization was therefore rigidly controlled. Flies were introduced in a chamber free of ether, ether was then applied for 60 seconds, and the flies taken for counting or weighing. This was enough to maintain the flies etherized for some 3 to 5 minutes.

The serial transfer technique allows easy measurement of the productivity and population size under controlled conditions. Natural selection is intense, both among the larvae and among the adults, since the populations reach a large size due to the continuous addition of newly born flies. The birth and death processes can be examined quite independently of each other.

RESULTS

Drosophila serrata: The total population counts for the two experimental populations and the control at 25°C are given in Figure 1. The populations were started with 1200 individuals, which is close to the equilibrium level for the control population. The size of the two experimental populations dropped considerably during the first five or six weeks. From the sixth week on, the experimental populations increased sharply in size. From the 10th week until the end of the experiment both irradiated populations maintained a size considerably larger than the control. Experimental population 1 reached a peak of about 2300 flies by the 15th week, and thereafter oscillated around that level in a pattern that is characteristic of this type of population. Experimental population 2 reached a peak of some 3000 flies by the 19th week, and oscillated around that level thereafter.

The productivity of the populations follows a similar pattern. During the 5th week the productivity of the control population was 650 flies versus 200 and 320 for experimental populations 1 and 2 respectively. From the 11th week onwards each of the irradiated populations produced more flies per week than the control.

Under the conditions of the experiment, the chromosome aberrations and highly deleterious dominant mutations induced during the first two radiations must have been for the most part eliminated before the start of the populations. The considerable decrease in size and the small productivity of the experimental populations during the first few weeks are caused by the elimination of dominant lethals and sublethals induced during the third treatment, and presumably due to the elimination of other mutants, the carriers of which are at a disadvantage under the conditions of strong competition.

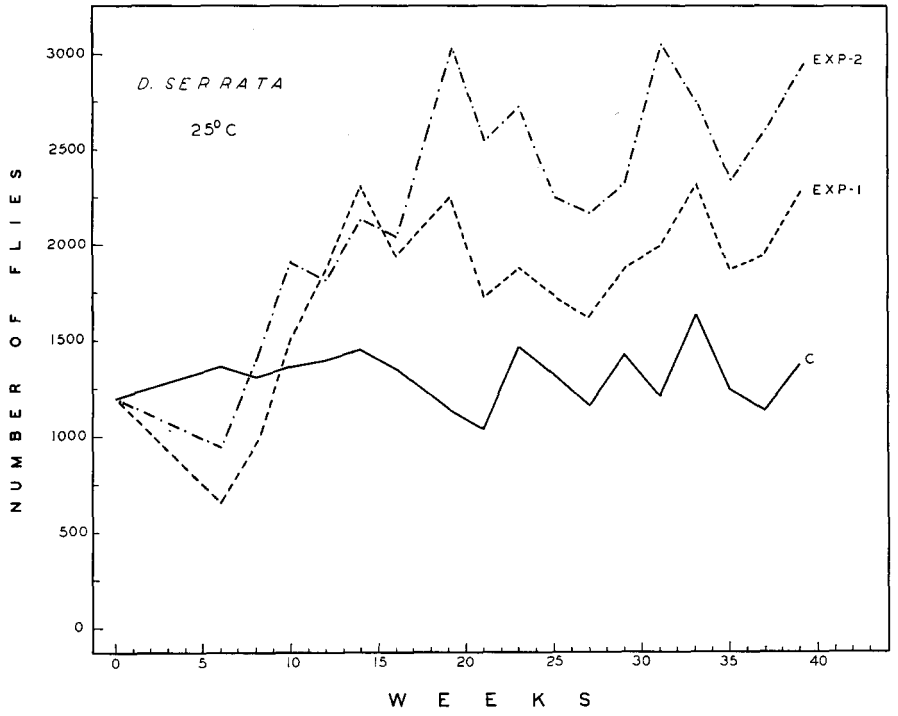

FIGURE 1.—Size of three experimental populations of *Drosophila serrata* at 25°C. C, the control population; Exp-1 and Exp-2, the irradiated populations.

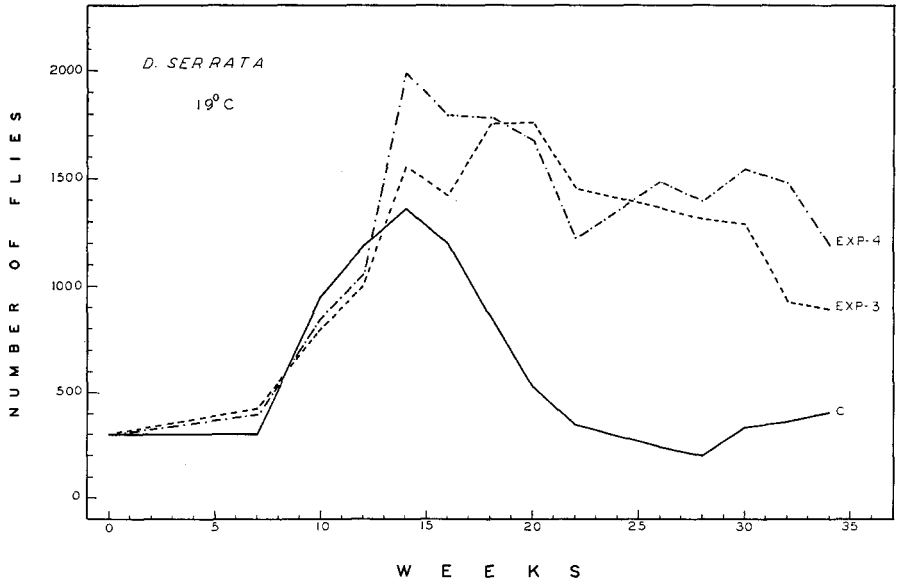

FIGURE 2.—Size of three experimental populations of *Drosophila serrata* at 19°C. C, the control population; Exp-3 and Exp-4, the irradiated populations.

TABLE 2

Mean production and population size of six experimental populations of D. serrata*

Population	Individuals produced per week†	Biomass produced per week (mg)‡	Newborn weight (mg)‡	Population size§	Population biomass (mg)§	Adult weight (mg)§
Control 1	595±21	315.5±27.3	.548±.006	1294±50	867.5±31.5	.672±.009
Experimental 1	941±30	526.5±22.4	.556±.007	1955±65	1308.7±48.2	.669±.009
Experimental 2	1133±27	613.6±20.1	.540±.006	2558±98	1676.2±59.9	.651±.009
Control 2	236±28	131.5±13.4	.586±.028	498±110	352.2±67.3	.735±.006
Experimental 3	499±19	307.5±17.3	.595±.009	1358±102	956.3±68.1	.706±.010
Experimental 4	519±18	327.2±15.3	.589±.014	1515±75	1055.9±34.6	.702±.014

* Mean production from week 13 until the end of the experiment; population size from week 16 until the end of the experiment.
† Number of measurements=28 at 25°C, and 21 at 19°C.
‡ Number of measurements=13 at 25°C, and 9 at 19°C.
§ Number of measurements=12 at 25°C, and 9 at 19°C.

On the 51st day after the populations were started, a sample of 300 flies was taken from each population to begin the derived populations at 19°C. The total population counts for these populations are presented in Figure 2. Flies start to hatch during the 4th week, and until the 7th week the newborn flies are barely able to replace the dead ones. A sharp increase occurs afterwards. The sizes of the control and the experimental populations are approximately equal until the 12th week. Thereafter the experimental populations maintain a considerably larger size than the control. All the populations reach peaks on the 14th week, and then drop to what seems to be an equilibrium level. The productivity follows a similar pattern, both experimental populations producing more flies per week than the control from the 12th week onwards.

Table 2 presents, for the six populations of *D. serrata*, the means and their standard errors for the following parameters: number of flies produced per week; biomass produced per week; individual weight of newborn flies; number of flies in the adult population; biomass of the adult population; average weight of an adult fly. The weights of single flies are calculated from the collective weighings. The means are calculated for the measurements made from the 13th week until the end of the experiment for the newborn flies, and from the 16th week on for the adult population. The difference in productivity and size between the control and the experimental populations is highly significant. Experimental population 2 is significantly superior to experimental population 1 at 25°C. The individual weights are not significantly different, so that differences in numbers and in biomass are of the same order. There seems to be, however, a decline of adult weight in the larger populations, presumably due to the greater difficulty that the flies encounter to feed in the more crowded bottles.

Drosophila birchii: The populations at 25°C were started with 1200 individuals, which seems to be over the level of equilibrium of the control population. It can be seen in Figure 3 that the control as well as the experimental populations decrease in size down to 500 to 600 individuals by the 6th week. From that point on, all populations increase gradually in size until the end of the experiment,

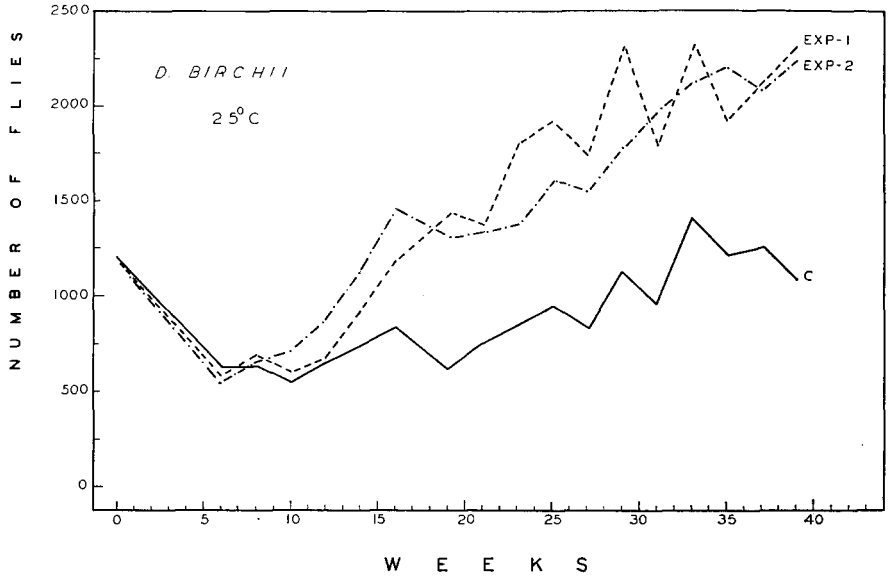

FIGURE 3.—Size of three experimental populations of *Drosophila birchii* at 25°C. C, the control population; Exp-1 and Exp-2, the irradiated populations.

the increase being the greatest in the experimental populations. From the 8th week on the size of the experimental populations has been consistently superior to that of the control.

The productivity of the control population was initially high; during the 4th week the control population produced 520 flies versus 240 and 100 produced by experimental populations 1 and 2 respectively. From the 5th to the 12th week productivity was approximately the same for the three populations. From the 13th week onwards the experimental populations have consistently produced

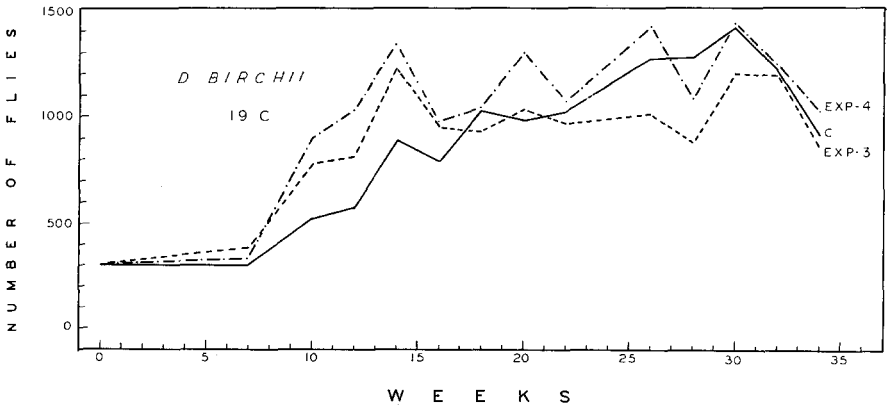

FIGURE 4.—Size of three experimental populations of *Drosophila birchii* at 19°C. C, the control population; Exp-3 and Exp-4, the irradiated populations.

more flies than the control. There seems to be a continuous rise in the productivity of the experimental populations from the 13th week on, but not in the control.

The population counts of *D. birchii* at 19°C are presented in Figure 4. These populations were derived from the 25°C populations by taking a sample of 300 flies from each one of them which became the founders of the new populations. The three populations maintain approximately the same size until the 7th week. The two experimental populations increased sharply at that point, reaching a peak of approximately 1250 flies by the 14th week, and thereafter oscillated around that level, with experimental population 4 being consistently above experimental population 3. After the 7th week, the control population increased in size at a slower rate than the experimental ones, so that for the next 10 weeks its size was appreciably smaller than that in the experimental populations. The increase in size of the control, however, has continued for most of the experimental period; from the 18th week on its size approximately equalled that in the experimental populations. The productivity followed a similar pattern, the control population being inferior until the 15th week, and approximately equal to the irradiated populations from the 16th week on.

Table 3 gives for the *D. birchii* populations the same parameters as Table 2, and for the same periods. The mean productivity and the mean sizes of the experimental populations at 25°C are significantly larger than the control means. The average individual weights are not significantly different, so that the differences in numbers and in biomass are of the same order. There is no significant difference between the two experimental populations.

At 19°C there is no significant difference in mean size among the populations. The productivity of experimental population 4 is significantly larger than that of the control ($t=2.6$, $P<.02$) and of experimental population 3 ($t=2.3$, $P<.05$); the difference between experimental population 3 and the control is not significant.

Regression analysis: A regression analysis on time of the differences between the experimental populations and the controls in size and in number of flies

TABLE 3

Mean production and population size of six experimental populations of D. birchii*

Population	Individuals produced per week†	Biomass produced per week (mg)‡	Newborn weight (mg)‡	Population size§	Population biomass (mg)§	Adult weight (mg)§
Control 1	533±22	275±15	.520±.005	992±67	651±39	.656±.006
Experimental 1	933±32	497±36	.531±.012	1800±167	1223±81	.659±.008
Experimental 2	833±31	457±31	.542±.006	1756±103	1149±70	.653±.007
Control 2	473±28	304±26	.633±.015	1111±68	839±46	.758±.007
Experimental 3	495±16	305±16	.634±.011	1015±44	766±35	.755±.006
Experimental 4	557±29	325±20	.619±.012	1169±61	852±42	.730±.007

* Mean production from week 13 until the end of the experiment; population size from week 16 until the end of the experiment.
† Number of measurements=28 at 25°C, and 21 at 19°C.
‡ Number of measurements=13 at 25°C, and 9 at 19°C.
§ Number of measurements=12 at 25°C, and 9 at 19°C.

TABLE 4

Regression on time of the difference in productivity and in size between the irradiated populations and the controls of D. serrata, *using weeks as time units*

	Productivity				Population size			
	$\bar{Y}$	b	t	P	$\bar{Y}$	b	t	P
Experimental 1—Control	254	11.4±4.1	2.78	<.01	493	26.0±8.5	3.05	<.01
Experimental 2—Control	399	18.3±4.4	4.15	<.001	972	41.3±10.4	3.97	<.01
Experimental 3—Control	198	10.1±3.5	2.89	<.01	594	36.1±14.0	2.58	<.05
Experimental 4—Control	212	15.6±2.2	7.08	<.001	740	45.7±10.5	4.35	<.01

$\bar{Y}$, mean difference; b, coefficient of regression of the differences; t and P for the significance of regression.

produced per week was done for the entire experimental period. The difference between each experimental population and its control was obtained for each measurement and the regression analysis made using weeks as time units. Table 4 presents for the *D. serrata* populations the mean difference in population size; the regression coefficient of the differences in size with its standard error; the mean difference in productivity per week; and the regression coefficient of the differences in productivity with its standard error. P and t values are given for the significance of the regressions. All the regression coefficients are positive, and significantly different from zero. The fitness of the irradiated populations, as measured by their productivity and size, has evolved continuously at a faster rate than the fitness of the controls. The slope of the differential increase is most pronounced during the first half of the experiment. Owing to the relatively small number of measurements available, no attempt was made to fit two regression straight lines crossing or a quadratic curve to the data.

Table 5 presents for *D. birchii* the same parameters as Table 4. At 25°C the differential increase in size of the two experimental populations is highly significant. The increase has been more gradual than in *D. serrata*, which is reflected in the smaller standard errors of the coefficient of regression of *D. birchii*. The differential increase in productivity has a positive regression coefficient for both experimental populations, but it is significantly different from zero only for experimental population 1. At 19°C the differences in productivity and size be-

TABLE 5

Regression on time of the difference in productivity and in size between the irradiated populations and the controls of D. birchii, *using weeks as time units*

	Productivity				Population size			
	$\bar{Y}$	b	t	P	$\bar{Y}$	b	t	P
Experimental 1—Control	290	17.5±4.2	4.16	<.001	621	35.1±5.2	6.73	<.001
Experimental 2—Control	221	12.9±9.4	1.37	>.10	587	29.6±3.2	9.23	<.001
Experimental 3—Control	47	−5.5±2.8	1.96	>.05	3	−16.9±5.3	3.20	<.01
Experimental 4—Control	101	−5.5±2.6	2.11	<.05	142	−13.6±5.8	2.34	<.05

$\bar{Y}$, mean difference; b, coefficient of regression of the differences; t and P for the significance of regression.

tween the experimental populations and the control have a negative slope, which is significantly different from zero in three cases, and is at the edge of significance for the productivity of experimental population 3. This reflects the higher original performance of the derived irradiated populations of *D. birchii* at 19°C, which was matched by a more steady increase of the control population.

The difference between the coefficients of regression for population size and the coefficients of regression for productivity is statistically significant for every population of *D. serrata* and for the populations of *D. birchii* at 25°C. That is, the differential rate of increase of the experimental populations is larger for population size than for productivity. AYALA (1965b) has shown that the evolution of population size occurs more readily than that of productivity. A selection for utilization of food has presumably occurred in the past for these strains in their natural habitats, while it is unlikely that the limitation of the available living space was ever so acute as in the experimental environment. Adult crowding is a new environmental factor for these flies, and evolutionary adaptation to it by incorporation of favorable genes or gene complexes occurs more readily.

Why there was no improvement in the fitness of the irradiated populations of *D. birchii* at 19°C is hard to tell. The randomly radiation induced genetic variability need not be beneficial for every population similarly treated. On the other hand, the *D. birchii* strain had been adapted to the 19°C temperature for some 35 generations previous to the experiment. Natural selection may have produced a well adapted genotype, so that the likelihood of further improvement at that temperature was considerably reduced. The *D. serrata* strain had been adapted to the 19°C condition for half that period only.

Longevity: The mean longevity of the adult flies is given in Table 6 .The estimation of the longevity has been described by AYALA (1965a). A crude estimate of longevity, *a*, is obtained dividing the mean population size by the mean number born per day. The flies are not added to the population continuously but at fixed intervals, two or three times a week, and the population is counted just prior to their addition. Therefore, a correction factor, *m-a*, is necessary. The values of *a* are at 25°C about 15 days for *D. serrata*, and vary from 13.05 to 14.76 days for *D. birchii*. The correction factor, *m-a*, equals 0.78 days for both species,

TABLE 6

Estimated mean longevity, in days, of the adult flies in the population

Population	*D. serrata*			*D. birchii*		
	a	*m—a*	*m*	*a*	*m—a*	*m*
Control 1	15.22	0.78	16.00	13.05	0.78	13.83
Experimental 1	14.59	0.78	15.37	13.53	0.78	14.31
Experimental 2	15.79	0.78	16.57	14.76	0.78	15.54
Control 2	14.65	2.12	16.77	16.34	2.13	18.47
Experimental 3	19.13	2.14	21.27	14.30	2.12	16.42
Experimental 4	20.47	2.15	22.62	14.61	2.12	16.73

a, crude estimate of longevity; *m—a*, correction factor; *m*, corrected mean longevity.

with two decimal accuracy. At 19°C the crude estimates of longevity range from 14.65 to 20.47 days for *D. serrata* and from 14.30 to 16.34 days for *D. birchii*. The correction factor at 19°C varies from 2.12 to 2.15. The most notable fact is the considerable increase in the longevity of the irradiated populations of *D. serrata* at 19°C.

The values of *a*, *m-a*, and *m* (the corrected mean longevity) are listed in the table. It should be noted, however, that the mean longevities as given in the table are measured from the time the flies are added to the crowded cultures. On the average, flies when added to the adult population are 1.17 days old at 25°C and 1.75 days old at 19°C.

DISCUSSION

According to WALLACE (1959), "viability improvements as a result of random mutation need not be a rare event if heterosis is a common phenomenon". He demonstrated in *D. melanogaster* that heterozygosity for radiation induced mutations may increase the average viability of otherwise homozygous individuals (WALLACE 1957, 1958, 1959). In a more recent experiment (1963) he shows that, as could be expected, the heterozygosis for radiation induced mutations lowers the viability of already heterozygous individuals. If a locus is already heterozygous for two different naturally occurring alleles, the substitution of a randomly induced allele for one of the naturally occurring ones is on the average detrimental, since the naturally occurring alleles had been exposed to natural selection. CRENSHAW (1965) has extended WALLACE's results to the flour beetle *Tribolium confusum*. In an inbred strain, the female progeny of irradiated males bearing the induced mutations in a heterozygous state produced significantly more viable offspring than control female progeny of nonirradiated males.

DOBZHANSKY and SPASSKY (1947) exposed to selection seven strains of *D. pseudoobscura* which were known to be homozygous for second or for fourth chromosomes carrying recessive genes or gene complexes deleterious to the flies. In one series of experiments, these strains were treated in such a way that natural selection favored mutations or gene combinations that improved the viability of the flies. In another series of experiments, the same chromosomes were "balanced" in such a way that natural selection was not operative. 1000r of X rays were administered to the males in every generation for 50 generations. Of the seven strains submitted to natural selection, six showed appreciable gains in viability, and one was unchanged at the end of the experiment. Recessive lethals and semilethals appeared in five of the balanced strains, while two strains were unchanged or slightly improved. The newly induced random mutations must have been on the average the same in both series, but in the first one any genetic variants which improved the viability were favored by natural selection. These experiments showed that, under the action of natural selection, living populations may not only eliminate the deleterious mutants induced by X-radiation but may undergo progressive improvement. However, the improvement was not faster or greater in the irradiated series than in a third series not irradiated but equally submitted to natural selection in spite of the larger amount of genetic variability

available to the former. DOBZHANSKY and SPASSKY speculated that 1000r per generation may have been excessive. The treated flies were, so to speak, flooded with deleterious induced mutations, and "the difficulty of eliminating this mass of degenerate germ plasm barely permitted the treated flies to keep their own in the race for viability improvements with the untreated homozygous strains".

An excessive amount of radiation applied to a relatively small population may have also been the reason for lack of sustained increase in fitness in the experiments by CARSON (1964) with *D. melanogaster*. Using a serial transfer technique rather similar to that in the present experiments, CARSON administered to two populations a total of 65,000r of X-radiation over 2½ years, in a single dose of 1000r or in two doses of 500r per week. That amounts to at least 2000r per generation during the radiation periods. The control population maintained an average size of slightly over 100 flies. During most of the radiation periods, the radiated populations maintained a population size of about half that number. The proportion of unconditionally deleterious mutants induced by such doses of radiation is expected to be considerably larger than that of potentially beneficial mutants. Since the flies were submitted to a strong competition immediately after the radiation treatment, there was little opportunity for genetic recombination. The probability of potentially beneficial mutants being induced without being associated with seriously deleterious ones in the same chromosome or individual, and eliminated with them, must have been small, given the small size of the experimental populations. Nevertheless, one of the irradiated populations showed superior fitness for a short time first, between weeks 49 and 58, until it was depressed by a new period of radiation treatment, and again after the last treatment for a much longer period, from weeks 114 to 145. From the figures and data given by CARSON, it seems, however, questionable whether that population had still a higher average fitness than the control during the last 15 weeks of the experiment (weeks 145 to 160).

In the present experiments a relatively large number of flies were irradiated for three generations, giving to the males a dose of 2000r per generation under conditions of relaxed selection. Only highly deleterious mutants and chromosomal aberrations are expected to be eliminated under these conditions, giving an opportunity for genetic recombination of the newly induced genetic variability before the flies are exposed to strong natural selection. Mutants that may not have been beneficial to their carriers on the genetic background in which they arose, may have formed new combinations of higher fitness. The depression occurring at the beginning of the experimental period shows that several generations have to elapse before superior genotypes can be selected and spread; the genetic burden imposed by the radiation outweighs its possible benefits during the first few generations.

AYALA (1965a) has shown that experimental populations started by mass hybridization between geographically widely separated strains of *D. serrata* had, after selection, higher fitness than the single-strain parental populations. In a *D. birchii* hybrid population a sudden sharp increase in fitness was observed, presumably due to appearance and multiplication of a new highly beneficial gene

combination. The average productivity of hybrid populations was, after equilibrium, about 29% superior to that of the single-strain parental populations, and their size was about 35% larger (AYALA 1966). Moreover, it could be demonstrated (AYALA 1965b) that the rate of evolution of hybrid populations was considerably superior to that of the single strain parental populations. The increase in the genetic variability responsible for the improvement in fitness was obtained, in those experiments, by mass hybridization, that is by the addition of two naturally selected though presumably not mutually coadapted gene pools. In the present experiments, the genetic variability is increased by high frequency radiation, and it seems apparent that, with natural selection, that increase can also result in an increase in the fitness of "normal" populations. Whether a similar increase could also be obtained in a natural population endowed with abundant genetic variability is questionable. The fact that the experiment was carried out under environmental conditions different from those in which the populations live in nature may have facilitated the selection of genotypes well adapted to the new laboratory conditions. The role of the radiation may have been to increase the genetic variability, resulting in an increase of the rate of evolution of the population in its adaptation to the new environment.

Finally, let it be clearly noted that the fitness improvements produced by radiation in the present experiments have no application to the human species, with its long generation time and its reduced reproductive capacity. Moreover, human values would hardly allow for the enormous price in lives and physical misery that the species would have to pay for such hypothetical improvement of its genetic endowment.

I take the pleasure of acknowledging the guidance provided by PROFESSOR TH. DOBZHANSKY throughout this investigation. I am also indebted to PROFESSOR HOWARD LEVENE for statistical advice; to MR. DAVID MARSDEN for irradiating the populations; and to MRS. SUZANNE MOSBY who did part of the calculations.

SUMMARY

Drosophila serrata and *D. birchii* flies were X-irradiated with 2000r per generation for three generations. Two experimental populations of irradiated flies and one control population were started for each species at 25°C. After 51 days a sample of 300 flies was taken from each population to start six other populations at 19°C. The populations were maintained under conditions of intense competition, both among the larvae and among the adults. At 25°C, the irradiated populations of *D. serrata* decreased in size and in productivity during the first few weeks of the experiment. From the 6th to the 15th week they increased greatly in size and in productivity, and maintained their superiorities until the end of the experiment. The equilibrium levels were 50 or more percent higher than that of the control. At 19°C the two irradiated populations of *D. serrata* were also superior to the control in productivity and in size from the 13th week until the end of the experiment. The two irradiated populations of *D. birchii* at 25°C increased in size steadily from the 5th week until the end of the experiment, exceeding the control population in productivity and in size by more than 50%.

At 19°C there is no marked difference between the control and the irradiated population.—Regression analysis shows that there has been a continuous differential increase in the fitness of the irradiated populations of *D. serrata* at both temperatures, and in those of *D. birchii* at 25°C. It is concluded that an increase in genetic variability produced by high frequency radiation may, with natural selection, result in an increase in the rate of evolution of the population, and finally of the fitness of the population in new environments.

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