GENETIC LOADS IN IRRADIATED EXPERIMENTAL POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*¹

EDUARDO TORROJA²

The Rockefeller Institute, New York City

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GENETIC changes induced by ionizing radiations have been studied much more at the level of individuals than at that of populations. The information available on the frequencies of different types of changes induced by various kinds of radiation exposure is quite extensive, relative to our knowledge of the destinies of these changes in the gene pool of the populations in which they occur. Many of the mutations that arise are deleterious to their carriers both in homozygous and in heterozygous condition, and therefore the fitness of the population is usually reduced by radiation exposures. It has nevertheless been shown, particularly by WALLACE (1956, 1962), BONNIER, JONSSON and RAMEL (1958), MOURAD (1962), CHUNG (1962), and SANKARANARAYANAN (1964), that populations with radiation histories return to approximately normal fitness levels if they are exposed to the action of normalizing natural selection for several generations after the radiation is discontinued. The processes which occur during this recovery are, however, very little understood.

In particular, it is desirable to study the fate of the mutational and of the balanced components of the genetic load. Some of the genetic changes that arise are close to neutral, and others are deleterious or heterotic in heterozygous condition. There are two possible approaches to such a study. First, genetic techniques are available in some species of *Drosophila* to obtain individuals carrying in double dose certain chromosomes extracted from the populations to be studied. A census can thus be made of the chromosomes that are lethal, semilethal, or quasi-normal when homozygous. Secondly, one may compare the viabilities of outbred and inbred progenies; the latter are expected to be less fit than the former if a population carries a concealed genetic load. MOURAD (1964) has used the first approach to study the genetic loads in certain populations of *Drosophila pseudoobscura* with radiation histories. The work to be reported in the present article used chiefly the second approach.

MATERIALS AND METHODS

Four experimental populations of *D. pseudoobscura* have been used in the present work. Three of them (2, 5 and 8) have been described by MOURAD (1962, 1964), and the fourth, the Control Population 211, by DOBZHANSKY, LEWONTIN and PAVLOVSKY (1964). Very briefly, the nature of these populations is as follows: No. 2 was started in February 1960, with founders

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² Present address: Genetics Foundation, Department of Zoology, University of Texas, Austin.

representing the F_1 generation of flies carrying the AR gene arrangement in their third chromosomes exposed to 16,000r of X rays, crossed to untreated flies with the CH gene arrangement. No. 5, started simultaneously with No. 2, had founders representing the F_1 generation of CH flies exposed to 12,000r of X rays crossed to untreated AR flies. No. 8 was identical in origin with No. 2, but for nine generations between February 1960 and May 1961, it received the inflow of 20 percent of homozygous AR flies treated with 16,000r in each generation. Populations 2 and 5 received no artificial irradiation between February 1960 and February 1963, when the experiments on inbreeding were started for the present investigation. Population 8 received no radiation between May 1961 and February 1963. Population 211 was started in March 1961 with unirradiated AR/CH heterozygotes. The AR and CH strains in all the populations were exactly the same, derived from flies collected at Piñon Flats, Mt. San Jacinto, California. And finally, to study the genetic loads carried by Populations 2, 5 and 8 at the beginning of their careers, AR males from all the base strains were given 16,000r of X rays, crossed to unirradiated CH females, and a number of single-pair matings were established from the progeny. In the following generation (i.e., two generations removed from the irradiated parents) brother $\times$ sister matings and matings of unrelated parents were arranged.

RESULTS

Viability in outbred and inbred progenies: The experiments to study the effects of inbreeding on the viability have been arranged following a modification of the technique used by DOBZHANSKY, SPASSKY and TIDWELL (1963) in their studies on natural populations. Virgin females and males hatching from the cups in a given population cage were taken, and 130 single-pair matings per population were arranged from them. From each of the single-pair progenies virgin females and male were collected, and three types of crosses were arranged, as follows: (1) Unrelated matings—groups of 10 females from a culture A with 10 males from a culture B, 10 females from B with 10 males from C, etc. (2) Brother-sister matings—groups of 10 females and 10 males from the same culture. (3) Half-sib matings—a single male was crossed with a group of 5 females from a culture A, and subsequently the same male was crossed to another 5 females from a culture B. From the two progenies groups of 10 females or 10 males (half-sibs) were taken and intercrossed.

The egg to adult viability was studied in the progenies of the above three types of matings. These progenies should have inbreeding coefficients, F , equal to 0, .25, and .125 respectively. The flies were placed in tubes with paper spoons containing a smoothly poured culture medium lightly smeared with yeast. Two samples of 50 eggs were taken from each progeny. In order not to disturb the eggs, sections of the culture medium with the eggs were cut out and transferred to culture bottles with the regular cream of wheat-molasses medium. All the cultures developed at 25°C.

The viability data are summarized in Table 1. This table shows the numbers of the egg samples in each class of matings with various percentages of the eggs, from 0 to 100 percent, surviving to the adult stage. It is strikingly apparent that the percentages of survival are much lower in the progenies of freshly irradiated flies (the "R" population, the lowermost part of Table 2) than in the progenies of the populations which were irradiated 3 years (Populations 2 and 5), or 2 years (Population 8) previously.

TABLE 1

Number of cultures with different percentages of survival from egg to adult stage

Population	F	0 0	1 4	5 8	9 12	13 16	17 20	21 24	25 28	29 32	33 36	37 40	41 44	45 48
2	0	..	..	..	..	..	..	..	..	..	..	..	..	..
	.125	..	..	..	..	..	..	..	..	1	..	..	..	..
	.25	..	..	..	..	..	..	..	..	..	..	..	..	..
5	0	..	..	..	..	..	..	..	..	..	..	..	..	..
	.125	..	..	..	..	..	..	..	..	..	..	..	..	..
	.25	..	..	..	..	..	..	..	..	..	..	1	..	1
8	0	..	..	..	..	..	..	..	..	..	..	..	..	..
	.125	..	..	..	..	..	..	..	1	..	..	..	..	..
	.25	..	..	..	..	..	..	..	..	..	1	2	..	..
211	0	..	..	..	..	..	..	..	..	..	..	..	..	..
	.125	..	..	..	..	..	..	..	..	..	..	..	..	..
	.25	..	..	..	..	..	..	..	..	..	..	..	..	1
R	0	5	9	4	11	9	8	6	6	2	5	8	3	..
	.25	3	8	12	11	5	12	3	8	7	3	3	9	4

Population	F	49 52	53 56	57 60	61 64	65 68	69 72	73 76	77 80	81 84	85 88	89 92	93 96	97 100	N
2	0	..	..	..	..	3	2	8	13	11	16	26	23	9	111
	.125	1	1	2	1	3	6	10	10	13	16	18	18	7	107
	.25	2	..	2	4	1	4	4	13	13	16	22	18	9	108
5	0	..	..	..	1	5	10	4	16	10	20	18	23	13	120
	.125	2	2	4	3	4	5	12	10	13	16	14	11	5	101
	.25	1	4	4	1	7	7	10	13	14	19	14	8	4	108
8	0	..	1	..	..	5	6	9	12	16	13	19	17	12	110
	.125	..	1	2	6	1	6	6	13	17	20	13	16	2	104
	.25	1	2	2	3	8	5	7	11	12	15	15	15	7	106
211	0	..	..	..	..	1	3	8	10	18	15	24	21	17	117
	.125	1	2	..	3	2	4	6	8	11	22	24	13	7	103
	.25	1	..	3	2	4	5	7	10	15	23	21	21	6	119
R	0	5	3	5	2	3	2	3	1	2	..	3	..	..	105
	.25	2	1	2	2	..	2	2	..	..	1	2	..	..	102

The mean percentages of survival are reported in Table 2. The control population, 211, shows an ostensibly higher survival than the others, but the differences are small and mostly not statistically assured. The R population is, as indicated above, much less viable. In all the populations, the outbred progenies ($F=0$) are, as expected, more viable than the progenies of the brother-sister matings ($F=.25$), and the half-sib progenies ($F=.125$) are ostensibly intermediate in three of the four cases. The differences are, however, remarkably small, much smaller than those observed by DOBZHANSKY, SPASSKY and TIDWELL (1963, Table 2), and by STONE, WILSON and GERSTENBERG (1963) in natural populations of *D. pseudoobscura*, and even more strikingly smaller than found by MALOGOLOWKIN, LEVENE, DOBZHANSKY and SIMMONS (1964) in natural populations of *D. willistoni*. To be more precise, the survival frequencies observed by all these authors in the outbred progenies are much the same as in my data, but their inbred progenies are much less viable.

TABLE 2

Percentages of eggs developing to the adult stage in outbred and inbred progenies

Population	$F=0$	$F=.125$	$F=.25$
2	86.98 $\pm$.76	83.58 $\pm$ 1.08	84.88 $\pm$.94
5	85.74 $\pm$.96	80.98 $\pm$ 1.16	79.52 $\pm$ 1.26
8	84.96 $\pm$.88	82.12 $\pm$ 1.04	81.28 $\pm$ 1.24
211	87.80 $\pm$.72	84.86 $\pm$ 1.00	84.46 $\pm$.90
R	31.44 $\pm$ 2.38		27.00 $\pm$ 2.10

The A and B statistics: MORTON, CROW and MULLER (1956) suggested two statistics, A and B , and their ratio, $B:A$, which, they believed, could discriminate between genetic loads of mutational and of balanced kinds. The A value is a measure of the mortality, i.e. the deviation from a perfect survival, in an outbred population, $F=0$. This mortality is due to a combination of genetic and environmental causes. The B value is intended to represent the number of "lethal equivalents" in a zygote arising through a doubling (homozygosis) of a chromosome set. These statistics have been calculated from my data with the aid of the method of weighted regression analysis kindly suggested by PROFESSOR HOWARD LEVENE, and described by him in MALOGOLOWKIN *et al.* (1964). The results are shown in Table 3. For comparison, similar calculations have been made from the data of DOBZHANSKY, SPASSKY and TIDWELL (1963) on four natural populations of *D. pseudoobscura* studied by them. The resulting figures are shown in Table 4, which is analogous to Table 3 in the paper of the authors just quoted.

The A value is very high in the freshly irradiated Population R (Table 3). In the other populations it is much lower, varying only from .133 to .163 in the experimental and from .108 to .203 in the natural populations (Table 4). A very similar range of values, .126 to .206 is found in the natural populations of *D. willistoni* by MALOGOLOWKIN *et al.* (1964, Table 3). Since the A value includes, as stated above, both the genetic and the environmental mortalities, this uniformity is rather remarkable, the more so since the extreme values are all subject to considerable sampling errors. The B values, supposedly measuring the concealed genetic loads, are, on the contrary, quite variable. They range (Table 3) from .163 in the control population and .111 in Population 2 to .311 and .321 in

TABLE 3

Estimates of the A and B values and of the B:A ratios obtained from the observed mortality rates in outbred and inbred progenies

Population	A	B	$B:A$
2	.1439 $\pm$.008	.1110 $\pm$.056	.77 $\pm$.42
5	.1568 $\pm$.010	.3206 $\pm$.072	2.05 $\pm$.55
8	.1627 $\pm$.010	.3113 $\pm$.073	1.30 $\pm$.51
211	.1328 $\pm$.008	.1630 $\pm$.053	1.23 $\pm$.45
R	1.1571 $\pm$.076	.6088 $\pm$.434	.53 $\pm$.40

TABLE 4

Estimates of the A and B values and of the B:A ratios in natural populations of D. pseudoobscura, calculated from the data of DOBZHANSKY, SPASSKY and TIDWELL (1963)

Population	A	B	B/A
M	.1387 $\pm$.033	.8758 $\pm$.257	6.31 $\pm$ 3.1
A	.2029 $\pm$.037	.6704 $\pm$.260	3.30 $\pm$ 1.59
B	.1083 $\pm$.020	.7971 $\pm$.180	7.39 $\pm$ 2.67
C	.1311 $\pm$.012	.4897 $\pm$.094	3.74 $\pm$.99

the population with radiation histories. The recently irradiated Population R has, as should be expected, a considerably higher value, .609. What is perhaps unexpected is that the *B* values in natural populations of *D. pseudoobscura* (Table 4) are higher than those in the populations with radiation histories, and even higher than in the recently irradiated population, the range being from .490 to .876. Even higher values are found in the natural populations of *D. willistoni* (Table 3, MALOGOLOWKIN *et al.*, 1964), the mean for all localities being 1.092. In other words, the loss of viability due to inbreeding is the greatest in wild *D. willistoni*, followed by the wild *D. pseudoobscura*, the recently irradiated *D. pseudoobscura*, and minimal in the experimental populations of *D. pseudoobscura* kept in laboratory population cages. It is, then, not surprising that the *B*:*A* ratios, which were once supposed to discriminate between the mutational and the balanced loads, are low in the experimental populations (.53 to 2.05), higher in natural populations of *D. pseudoobscura* (3.30 to 7.39), and still higher in *D. willistoni* (the average of 6.51).

Lethal and semilethal chromosomes: The loss of the viability observed in the inbred, compared to the outbred progenies, in the experimental populations is much smaller than it is in the natural ones. This seems to indicate that the experimental populations carry only small concealed genetic loads. This inference can be tested with the aid of the method of obtaining flies homozygous for certain chromosomes, by means of series of crosses in which the chromosomes are guided by the use of proper mutant gene markers. MOURAD (1964) has analyzed samples of second and third chromosomes from a freshly irradiated population (our Population R), and from Population 2; of second chromosomes from an unirradiated control (analogous to, but not identical, with Population 211); and of third chromosomes from Population 5. Further data for the second and third chromosomes from Populations 8 and 211 are reported in Table 5 and 6. The procedures utilized in these experiments were the same as in those of DOBZHANSKY and SPASSKY (1963) and MOURAD (1964), and need not be detailed here. The figures in Table 7 for the third chromosomes in Populations 2 and 5 have been calculated from MOURAD's data, taking into consideration the known frequencies of the AR and CH third chromosomes in these populations.

The data in Tables 5, 6 and 7 permit the following comparisons to be made. Excepting the recently irradiated population (R), in which more than half of the second and of the third chromosomes are lethal or semilethal when homozy-

TABLE 5

Viabilities, in percentages of the +/+ flies in the cultures, of the homozygotes and heterozygotes for second and third chromosomes from the experimental populations

Population	Chromosome	Percent												N
		0	2	4	6	8	10	12	14	16	18	20	22	
211	3rd, Homozygotes	7	2	..	..	..	..	1	2	..	..	2	3	3
211	2nd, Homozygotes	5	1	..	..	1	..	..	1	1	..	1	2	2
8	3rd, Homozygotes	2	7	..	..	..	..	..	2	..	..	1	2	4
8	3rd, Heterozygotes	..	..	..	..	..	..	..	..	..	..	1	..	..
8	2nd, Homozygotes	6	1	..	..	..	..	1	..	1	..	2	1	4
8	2nd, Heterozygotes	..	..	..	..	..	..	..	..	..	..	..	1	1

Population	Chromosome	Percent												N
		24	26	28	30	32	34	36	38	40	42	44	46	
211	3rd, Homozygotes	5	10	8	16	16	16	13	7	1	2	..	..	114
211	2nd, Homozygotes	6	7	9	19	15	16	11	9	2	..	1	..	109
8	3rd, Homozygotes	12	10	16	9	18	10	9	4	1	1	..	..	108
8	3rd, Heterozygotes	2	3	6	15	21	27	15	13	5	..	..	..	108
8	2nd, Homozygotes	7	10	18	18	20	8	5	3	1	1	..	..	107
8	2nd, Heterozygotes	3	6	7	16	19	26	16	10	4	2	..	..	111

TABLE 6

Mean viabilities in percentages of +/+ flies in the test cultures, and in viability ratios

Population	Chromosome	All chromosomes	Quasi-normal	Viability ratios	T values
211	3rd, Homozygous	28.73 ± .93	31.61 ± .51	.806 ± .088	.199 ± .052
211	2nd, Homozygous	29.53 ± .88	31.84 ± .49	.838 ± .076	.128 ± .047
8	3rd, Homozygous	27.57 ± .89	30.24 ± .48	.761 ± .077	.289 ± .049
8	3rd, Heterozygous	33.68 ± .36	..	1.016 ± .013	..
8	2nd, Homozygous	27.87 ± .86	30.16 ± .45	.773 ± .071	.264 ± .048
8	2nd, Heterozygous	33.40 ± .40	..	1.006 ± .016	..

gous, the experimental populations with or without radiation histories carry relatively few lethal chromosomes in comparisons with natural populations. DOBZHANSKY, HUNTER, PAVLOVSKY, SPASSKY and WALLACE (1963) record between 18.3 ± 2.7 and 33.0 ± 4.5 percent of lethal and semilethal second chromosomes, and between 13.9 ± 1.0 and 30.0 ± 4.2 percent of lethal and semilethal third chromosomes in various natural populations of *D. pseudoobscura*. In MOURAD's and my experimental and control populations, only 7 to 8 percent of the second and 4 to 10.5 percent of the third chromosomes are lethal or semilethal. In the populations with radiation histories the frequencies of lethal and semilethal chromosomes are only slightly, if at all, higher than in the control (Table 7).

Chromosomes that are subvital in double dose are also not numerous in the populations with radiation histories. Table 6 shows that the mean frequency of the wild-type (nonmutant) class in the test cultures in which this class is heterozygous for two different second chromosomes is $33.4 \pm .4$, and for two third chromosomes $33.7 \pm .4$ percent. Homozygosis for the second or for third chromosomes

TABLE 7

Percentages of second and third chromosomes that are lethal or semilethal in double dose in the populations studied

Population	Second chromosome	Third chromosome
Unirradiated (MOURAD)	7.3 ± 3.0	3.95 ± 1.3
Unirradiated 211	$8.3 \pm .7$	$10.5 \pm .9$
Recently irradiated (R, MOURAD)	57.7 ± 4.7	76.4 ± 4.5
2 (MOURAD)	10.4 ± 3.3	16.9 ± 1.4
5 (MOURAD)		7.7 ± 1.1
8	$8.4 \pm .7$	$10.2 \pm .9$

causes a significant, though not very striking, reduction of the frequencies of the wild-type class. However, if we disregard the lethal and semilethal chromosomes, the remaining quasi-normal second chromosomes give on the average $31.8 \pm .5$ percent wild type in the control and $30.2 \pm .5$ percent in Population 8; the quasi-normal third chromosomes give $31.6 \pm .5$ percent in the control and $30.2 \pm .5$ percent in Population 8. The average viability of quasi-normal homozygotes is, thus, significantly but not strikingly lower than that of the heterozygotes. DOBZHANSKY, SPASSKY and TIDWELL (1963, Table 5) give $29.1 \pm .05$ for the quasi-normal second, and $26.7 \pm .05$ for the quasi-normal third chromosomes from natural populations. This last figure is in error, 28.2 being more nearly correct.

An attempt may now be made to estimate the magnitude of the genetic loads in the second and third chromosomes of our populations, using the method devised by GREENBERG and CROW (1960), and used also by DOBZHANSKY, SPASSKY and TIDWELL (1963) and by MALOGOLOWKIN *et al.* (1964). Estimates of the viability of heterozygotes are available only for Population 8, but not for the control Population 211 (Table 6). For this last population, the mean viabilities of the heterozygotes given in Table 5 of DOBZHANSKY, SPASSKY and TIDWELL have been taken as the best approximations available. The *T* values turn out to be about $.13 \pm .05$ for the second and $.20 \pm .05$ for the third chromosomes in the control population, and $.26 \pm .05$ for the second and $.29 \pm .05$ for the third chromosomes in Population 8. The population with a radiation history shows, consequently, a higher, but not a significantly higher, load.

These estimates of the genetic loads may be compared with $.48 \pm .07$ for the second and $.57 \pm .07$ for the third chromosomes in the natural populations of *D. pseudoobscura* studied by DOBZHANSKY, SPASSKY and TIDWELL and recalculated by MALOGOLOWKIN *et al.* (1964). Their figure for the fourth chromosome is $.66 \pm .07$, giving the total load $1.72 \pm .12$. The fourth chromosomes have, unfortunately, not been tested in MOURAD's and my experiments, making it impossible to give precise estimates of the total load. If, as seems probable, the fourth chromosomes in our populations carry loads about equal or only slightly higher than found in the third chromosomes, the total loads will be only about half as large as in the natural populations. Even so, they will be appreciably larger than the estimates of *B* given in Table 3. To this extent, my data agree with these of

DOBZHANSKY, SPASSKY and TIDWELL (1963) and of MALOGOLOWKIN *et al.* (1964), in showing that the estimates of loads obtained from the inbreeding depression of the viability are much lower than those arrived at through study of individuals made homozygous for certain chromosomes.

DISCUSSION

The genetic loads found in the experimental populations of *Drosophila pseudoobscura* are considerably smaller than those found in the natural populations of the same species. This is equally true of the experimental populations which did and of those which did not have radiation histories, although the former have, as expected, somewhat greater loads. The two independent methods utilized for the study of the genetic loads, namely that of the viability depression in inbred as compared to outbred progenies, and of the loss of the viability in individuals made homozygous for certain chromosomes extracted from the populations, lead to the same conclusions. This state of affairs is understandable if one examines the histories of the experimental populations. These histories have been described by MOURAD (1962, 1964), and a brief summary will suffice here.

The ancestors of the flies used were collected on Mt. San Jacinto, California, in 1949. Progenies of single females were inbred for from one to three generations to obtain strains having either the Arrowhead or the Chiricahua gene arrangement in the third chromosomes. This inbreeding certainly was not sufficient to make the strains homozygous for all genes, but it doubtless resulted in elimination of some of the chromosomes that were lethal or otherwise deleterious in homozygous condition. Between 1949 and the beginning of the experiments in 1960, the strains were kept in regular culture bottles, mostly in a cold room at 16°, transferred to fresh cultures about once in six weeks. As shown by LEVENE and DOBZHANSKY (1958), such strains can retain considerable heterozygosis for gene arrangements, and presumably for recessive lethal and deleterious genes, provided that the latter are advantageous in heterozygotes.

A part of the founders of the Populations 2, 5 and 8 received a heavy radiation treatment (16,000 or 12,000r), and Population 8 received in addition an inflow of heavily irradiated immigrants for nine generations (see MATERIAL and METHOD). The irradiation has greatly increased the genetic loads, as shown by MOURAD (1964) and also by the figures in the "R" line in Tables 1, 2, 3 and 7. The newly induced deleterious genetic variability must have consisted chiefly of mutational variants that were detrimental both when homozygous and when heterozygous. This is shown most clearly by the fact that the *A* value is almost twice as large as the *B* value in the population two generations after the irradiation (Table 3). In other words, the expressed load is greater than the concealed load in the immediate progeny of heavily irradiated flies. The experiments of SANKARANARAYANAN (1964) on irradiated *D. melanogaster* bear this out also: the egg-to-adult viability is very low in the progenies of irradiated parents, but in a few generations after the radiation is discontinued, this viability returns almost to the level of the unirradiated controls.

MOURAD (1964) estimates that no fewer than 28 and no more than 37 genera-

tions have elapsed between the irradiation and the analysis of the populations for the inbreeding depression and the chromosome homozygosis. During this interval of time, the genetic loads in the populations with the radiation histories became reduced almost, though not quite, down to the level of the control Population 211 (Tables 1-3, 5-7). The most remarkable fact is that this level is lower, not higher, than it is in the natural populations of *D. pseudoobscura* from which the ancestors of the founders of our experimental populations came (Table 4; see also DOBZHANSKY *et al.*, 1963). While the small genetic load in the control population (No. 211) is most probably due to the history of inbreeding in its ancestry, such an explanation is certainly not applicable to the other populations. The experimental populations kept in the population cages of the type used in the present experiments contain generally more than 1000 adult flies, and as shown by PROUT (1954), the genetically effective population size in such experimental populations is of the same order of magnitude as the population count. Starting no more than one generation after they are founded, the experimental populations can in no way be said to be undergoing an appreciable inbreeding. While the genetic load which was present in these wild ancestors was reduced by inbreeding, this is not the case with the radiation-induced load.

Even after a heavy irradiation, the experimental populations do not return to an equilibrium genetic load found in natural populations. Instead, the genetic load is reduced to a level lower than in nature. The most satisfactory explanation of this fact is that the genetic variants composing the genetic loads in natural populations are not random samples of the genetic variants arising by mutation, or at least of those induced by irradiation. As pointed out by DOBZHANSKY (1964 and other publications), the mutants that are deleterious when heterozygous are eliminated by natural selection from populations relatively rapidly; deleterious mutants that are nearly recessive accumulate up to the frequencies equal to the square roots of the frequencies of their origins by mutation; and the heterotic mutants accumulate up to levels determined by the relative advantages and disadvantages of the heterozygotes and the homozygotes.

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SUMMARY

The genetic loads have been studied by two methods. First, the egg-to-adult viability has been determined in the progenies of matings in which the parents were full sibs, half sibs, or not closely related genetically. Secondly, the viability of individuals made homozygous for certain chromosomes by means of a series of crosses was measured in relation to that of their heterozygous siblings. The experiments conducted utilizing both methods lead to concordant results. The recently irradiated populations carry very heavy genetic loads, consisting mainly of genetic variants which are deleterious in heterozygous, and doubtless also in

homozygous condition. Some 28 to 37 generations after the irradiation is discontinued, the genetic loads are found very greatly reduced, in fact, reduced below the levels observed in natural populations. The genetic variants composing the genetic loads in natural populations are evidently not random samples of the variants arising by mutation under the influence of irradiation.

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