

EFFECTS OF RADIATION ON POPULATIONS OF *DROSOPHILA MELANOGASTER* WITH DIFFERENT GENETIC STRUCTURES

I. CHANGES IN FITNESS AND PRODUCTIVITY

By K. F. DYER*

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Abstract

It has been shown in previous work that heterozygotes between irradiated and non-irradiated populations of *D. melanogaster* experience a marked reduction in competitive ability. The effects of allowing the nucleus of a heterozygote gene pool to develop are here investigated and it is found that the total number emerging from a cage containing irradiated, non-irradiated, and heterozygote flies is considerably increased and the number of heterozygotes themselves shows almost a 100% increase. It is concluded that the opportunity given to the heterozygotes to form an integrated gene pool allows them to overcome much of their competitive disability.

Further experiments involving three irradiated populations and the three possible hybrids between them which could be formed at each generation showed that these hybrid populations, although having similar radiation histories and containing similar genetic material, had a competitive ability reduced by over half or even three-quarters in many cases, compared with the parental population.

It appears that it is the nature of the gene pool rather than its heterozygosity or the individual genes contained in it which largely determines the fitness and competitive ability of the population.

I. INTRODUCTION

One of the most fruitful concepts developed in population genetics in recent years is that of the integrated gene pool. This is the idea that, since local populations are the units of evolution, their gene pools as a whole are selected and evolve together and therefore become cohesive units. In a series of previously reported experiments on small irradiated populations of *Drosophila melanogaster* (Dyer 1969a, 1969b, 1969c) it was shown that the integrated gene pools which developed overcame many of the disadvantageous effects of irradiation and allowed the full expression of a proportion of the induced mutations. The competitive ability of such populations was well maintained compared with unirradiated control populations. Heterozygote populations, however, derived anew at each generation from irradiated and non-irradiated populations, had no chance to develop integrated gene pools and these showed a failure to incorporate any useful induced mutations and, most important, a drastically reduced fitness and competitive ability compared with either of their parental populations.

* Department of Genetics, Monash University, Clayton, Vic. 3168.

The present experiments represent two different methods of investigating this situation in more detail. Each compares the fitness and competitive ability of small irradiated populations of *D. melanogaster* which are allowed to develop an integrated gene pool with similar populations which are not. The results in each case provide striking illustration of the very great influence of an integrated gene pool in determining the evolutionary future of any Mendelian population.

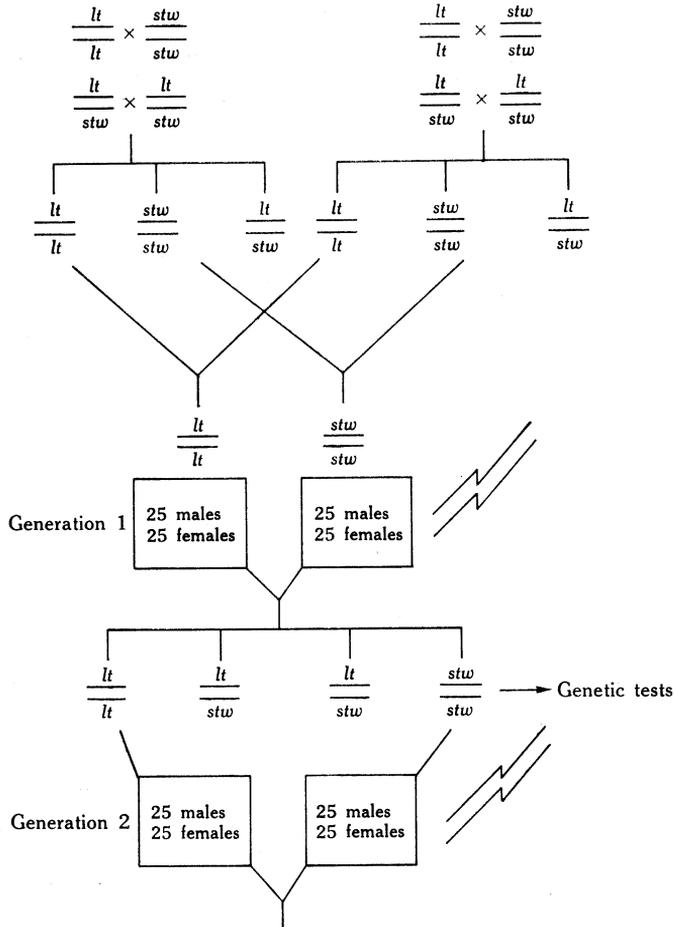


Fig. 1.—The experimental design.

II. MATERIALS AND METHODS

The basic plan of the experiment is shown in Figure 1, which shows the derivation, from two inbred lines, of two populations of flies which are genetically very similar but phenotypically distinguishable. The principal experimental details may be found in previous publications (Dyer 1969a, 1969b, 1969c). It suffices to say that at each generation the *straw* flies were irradiated with 1500 r X-rays and put into the same population cage as an equal number of unirradiated *light* flies. The three genotypes emerging, viz. *light*, *straw*, and heterozygotes between them, were collected and counted at each generation but, since only *light* and *straw* (using virgin females) were used for the next generation, the two populations retained their identity throughout the

experiments. Three series of experiments were run. Series 1 consisted of two population cages run for 25 generations and two subpopulations set up from these at generation 20. The first cage (CR) had all the *straw* flies irradiated; the second cage (CC) acted as control. The subpopulations were treated in exactly the same way except that, in addition to 25 males and females of *light* and *straw*, five *light/straw* heterozygote males and five virgin heterozygote females, which had hatched at the same time as the *light* and *straw* flies being used for this generation, were put into each of the population cages. Two cages were run, in one of them the *straw* flies were irradiated with 1500 r X-rays as before, the *light/straw* heterozygotes being unirradiated. The other cage served as the control. These two cages were designated RF and CF respectively. Both of these cages were run for five generations.

Series 2 experiments comprised three cages with *straw* irradiated (A, B, C) and two control (D, E) cages run for 12 generations. The three cages of series 3 were set up at each generation from the irradiated *straw* of series 2 populations by combining *straw* males from one population with *straw* females from another, irradiating, and then putting into a cage with an orthodox *light* population. They therefore had exactly the same accumulated radiation as series 2 populations, virtually the same genetic material, but non-integrated gene pools. These three populations were derived in all possible combinations from A, B, and C.

III. RESULTS

(a) Series 1

The introduction of five pairs of heterozygotes in cages RF and CF increased the number of flies by 10% compared with CR and CC and, since no alterations are made to the constitution of the gene pool, there should be a simple increase of 10% of all three emergent genotypes. This hypothesis is examined by comparing the two control populations, CC and CF, the results from which are shown in Table 1. In

TABLE 1
EFFECTS OF ALLOWING GENE FLOW BETWEEN TWO UNIRRADIATED POPULATIONS OF FLIES ON THE NUMBERS EMERGING

Generation		Total		<i>straw</i>		<i>light</i>		Heterozygotes	
CC	CF	CC	CF	CC	CF	CC	CF	CC	CF
21	1	1634	1675	758	497	279	277	597	901
22	2	1760	1970	1037	505	316	400	407	965
23	3	1774	1712	781	895	340	240	652	577
24	4	1808	1911	812	516	329	335	667	1060
25	5	1625	1447	665	505	437	275	523	667
Total		8601	8613	4053	2918	1701	1527	2846	4170
Mean		1720	1723	811	584	340	305	569	834

fact the total numbers emerging are not very different at any generation and the *light* and *straw* genotypes both show a small reduction in numbers emerging. On the other hand, the mean numbers of heterozygotes emerging is as much as 46.6% greater with the addition of these few extra flies than without.

The situation among the irradiated populations is inevitably complicated by the incidence of dominant and recessive lethals. As mentioned in earlier papers (e.g. Dyer 1966), 45% dominant lethals are induced among the *straw* flies prior to gene flow and it has also previously been shown (Dyer 1969a) that approximately

60% recessive lethals with a rate of allelism of about 15% will give rise to approximately 10% genetic deaths at each generation. Since there are, therefore, only about half the possible number of *straw* flies actually hatching, the contribution from the extra heterozygotes will be effectively doubled in proportionate terms, i.e. the extra 10% heterozygote flies introduced will give rise, approximately, to an extra 20% *straw* flies.

The number of heterozygotes emerging in cage CR are also reduced because of the induction of dominant lethals, in this case by about 25%. The introduction of 10% unirradiated heterozygotes will in fact mean that the expected difference between the numbers of heterozygotes in cages CR and RF is approximately 13%. The *light* flies do not suffer any induced genetic deaths and are therefore expected to show a simple 10% increase when the extra heterozygotes are added. The net overall increase in the total numbers of flies hatching from cage RF compared with cage CR is compounded of the contribution of all three genotypes and is expected therefore to be: 55 : 45 *straw*; 170 : 150 heterozygotes; 110 : 100 *light*; total 335 : 295, approximately 15%.

TABLE 2

EFFECTS OF ALLOWING GENE FLOW BETWEEN IRRADIATED AND UNIRRADIATED POPULATIONS OF FLIES ON THE NUMBERS EMERGING

Generation		Total		<i>straw</i>		<i>light</i>		Heterozygotes	
CR	RF	CR	RF	CR	RF	CR	RF	CR	RF
21	1	950	1212	230	290	380	402	340	520
22	2	1099	1637	162	401	650	576	287	660
23	3	1302	1834	213	492	640	642	449	700
24	4	1349	1975	376	349	752	731	217	895
25	5	1492	1412	395	354	695	549	372	509
Total		6188	8070	1376	1886	3117	2900	1665	3284
Mean		1238	1614	275	377	623	580	333	657

The actual results from these two irradiated populations are shown in Table 2. The mean total numbers emerging from the cage with heterozygotes included was 30.4% greater. The principal contributors to this increase in numbers emerging were the heterozygotes, which showed a 97.3% increase. These heterozygotes changed from forming 27% to forming 40% of the total emergence. The number of *straw* flies emerging from this cage increased by 37.1%, although this obviously did not form any important proportionate increase. The number of *light* flies on the other hand showed a mean decrease of 7.4%. The *light* flies therefore followed the behaviour of the two genotypes in the control population in cage CF, in which both *light* and *straw* showed a decrease in competitive ability after gene flow through the permanent heterozygote gene pool had commenced.

The most significant results from allowing gene flow appear to be in the irradiated population; the consequences of gene flow for these three genotypes are therefore shown in Figures 2(a)-2(c).

(b) Series 2

The three cages A, B, and C of these experiments showed some diversity of response. In particular, cage C became rather different from either A, B, or the first 12 generations of cage CR, regarding the number and proportion of *straw* flies emerging after generation 8. Populations A and CR, however, showed a close measure of agreement in that the *straw* flies had a modest proportional increase in emergence over these 12 generations. The most important result, though, was that all four cages showed the same pattern of behaviour in the number and proportion of heterozygotes emerging. It has already been shown (Dyer 1966) that there was a significant fall in the proportion of heterozygotes emerging over these 12 generations in cage CR.

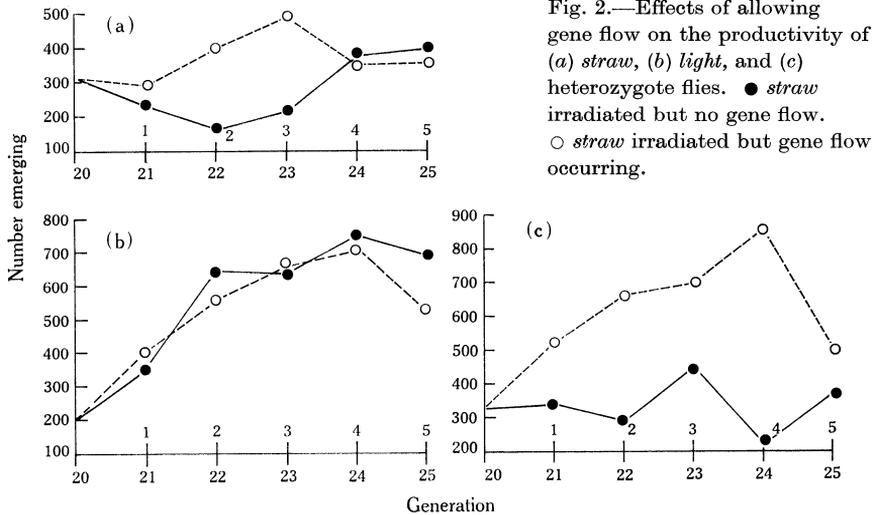


Fig. 2.—Effects of allowing gene flow on the productivity of (a) *straw*, (b) *light*, and (c) heterozygote flies. ● *straw* irradiated but no gene flow. ○ *straw* irradiated but gene flow occurring.

This fall was considerably more pronounced in all the repeat experiments of series 2, especially cage A. The increase in the proportion of *light* flies emerging was also common to all four cages. It therefore seems reasonably certain that the basic response described in Dyer (1969c) was common to them although each of these repeat populations shows certain variations, due to the small size of the populations employed and the severe radiation stresses applied.

In other words, without presenting the results in detail, the three populations of series 2 can be accepted as a confirmation of previous work and a valid series of comparisons for the hybrid populations of series 3.

(c) Series 3

In examining the results from the mixed populations we shall be concerned entirely with the results from the three *straw* populations. In the rather special circumstances of these experimental population cages the *light* and heterozygotes behaved quite normally and did not add materially to knowledge already gained from series 1 and 2.

If the formation of these composite populations had no effect on competitive ability, the numbers emerging would be approximately the mean of the number

emerging in each of the two parent populations. In view of the fact that inbreeding was completely eliminated in the composite populations, the losses due to homozygous recessive lethals would not occur and therefore the numbers emerging in the

TABLE 3

COMPARISON BETWEEN NUMBERS OF *straw* EMERGING IN THE THREE COMPOSITE IRRADIATED POPULATIONS AND THE MEAN OF THEIR TWO PARENTAL POPULATIONS

Gener- ation	Parental Flies from Cages A and B	Mean of Parental Popula- tions	Parental Flies from Cages A and C	Mean of Parental Popula- tions	Parental Flies from Cages B and C	Mean of Parental Popula- tions
1						
2	449	473	762	405	372	382
3	266	485	135	464	219	471
4	204	436	487	469	243	352
5	82	429	104	427	142	398
6	78	465	419	453	200	350
7	113	418	298	310	159	462
8	394	351	221	361	36	282
9	137	295	310	320	157	176
10	154	434	263	368	144	260
11	256	462	207	382	121	266
12	97	511	146	410	99	318
Total	2230	4859	3352	4373	1892	3717
Mean	203	442	305	398	172	338

composite populations might be expected to be marginally greater on this account. With lethal frequencies up to 50% and allelism levels approaching perhaps 10% (Dyer 1969*a*) this is quite an important factor.

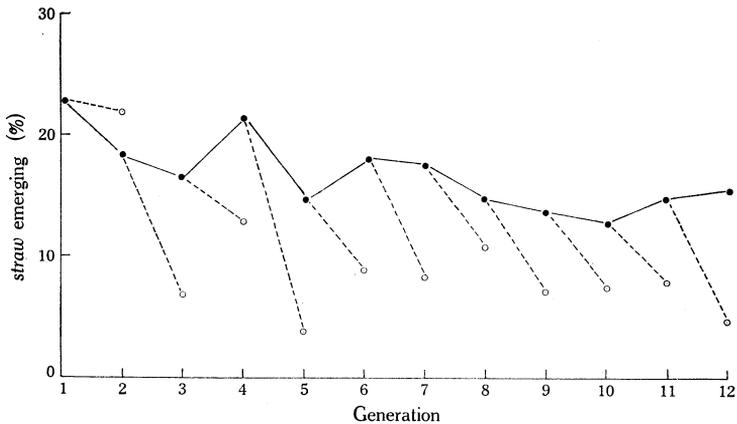


Fig. 3.—Mean percentages of *straw* hatching from the three normal populations at each generation (●) and from the composite populations (○).

The comparisons between each of the three composite populations and the mean of their two "parental" populations are shown in Table 3. In all three populations

and at every generation except the eighth in cages A and B, the third in cages A and C, and the first generations in all three, the numbers emerging from these composite populations are considerably lower than the mean of their parents. In some cases there are half as many flies emerging, in some cases one-quarter as many, and in several cases less than one-quarter. It is beyond question that, whatever the performance of normal irradiated populations, first-generation hybrids between them have a drastically lower competitive ability. To emphasize this particular finding, the mean percentages of *straw* hatching from the three normal populations at each generation are plotted in Figure 3 together with the mean percentage of *straw* hatching from the composite populations. The differences are impressive. There were no important differences in the total number of flies emerging from the two sets of cages A, B, C, and their hybrids which could have been contributory causes, and the single composite control population which was run was always in broad agreement with the mean of the two normal control populations from which it was derived (Table 4).

TABLE 4

COMPARISON BETWEEN THE MEAN NUMBERS OF *straw* EMERGING FROM THE COMPOSITE CONTROL POPULATION AND THE MEAN OF ITS TWO PARENTAL POPULATIONS

Gener- ation	Parental Flies from Cages D and E	Mean of Parental Populations	Gener- ation	Parental Flies from Cages D and E	Mean of Parental Populations
1			7	924	538
2	483	584	8	1,366	638
3	866	794	9	1,695	1,192
4	1,689	920	10	1,459	1,102
5	811	1,149	11	1,503	982
6	690	856	12	1,063	882
Total				12,549	9,637
Mean				1,141	876

IV. DISCUSSION

The concept and importance of the integrated gene pool in population genetics is now almost universally recognized. The behaviour of the *light/straw* heterozygotes in series 1 and 2 experiments is worthy of further emphasis in this context. As members of a discontinuous population they are at a severe disadvantage and their competitive ability is greatly reduced by the effects of radiation-induced mutations. The addition of just 10 complete genotypes at each generation, in themselves capable of producing only about 10% of the total number of heterozygotes, is clearly sufficient to form a nucleus around which an integrated gene pool can form and lead to a doubling of the number emerging. The heterozygotes from the "irradiated" cage RF are still at some disadvantage compared with the control CF and to this extent this small nucleus is incapable of successfully absorbing all the new mutations introduced. Nevertheless, the observed transformation of these heterozygotes within the span of five generations is impressive, and is worthy of further investigation as a possible useful method of utilizing radiation-induced mutants in animal and plant breeding.

The irradiated *straw* population itself benefits from this slightly enlarged gene pool and the genetic exchanges associated with it. The *straw* flies now show no detrimental effects at all from the radiation, and this too may be of some practical significance in possible improvement programs.

A number of other situations have been investigated where gene flow between two diverging populations is occurring; the results suggest that it may act as an important means whereby major genetic reconstructions can be carried out in sub-populations without drastic effects on fitness and viability. Thus, Streams and Pimental (1961) found that with a high degree of selection genetic differentiation could still occur despite gene exchange. Thoday and his co-workers (Thoday and Boam 1959, 1961; Millicent and Thoday 1960, 1961) quantified such results and showed that up to 25% gene flow between two selected materials did not materially affect the degree of divergence as measured by sternopleural chaeta number in *Drosophila*; even up to 50% gene flow could still allow divergence. In natural populations of various grasses, Bradshaw and his colleagues (Bradshaw, McNeilly, and Gregory 1965; Aston and Bradshaw 1966; and Jain and Bradshaw 1966) have shown that considerable differentiation occurs in certain plant populations due to environmental differences, particularly in the case of heavy metallic contamination, despite gene flow at very high levels due to pollen transfer. All of these results emphasize the supreme importance of the population gene pool as the controller of its evolutionary destiny, and that fitness and evolutionary advance can be maintained provided a portion of the gene pool is retained in a functional form.

The results presented in this paper were foreshadowed in the experiments of Wallace and Vetukhiv (Wallace 1955; Wallace and Vetukhiv 1955; Vetukhiv 1957), who laid the foundations for a considerable volume of subsequent work. The particularly severe genetic stresses produced by heavy irradiation in every generation demonstrate the phenomena associated with integrated gene pools in a particularly striking way, albeit in small populations. Further work (Dyer 1971) has extended this over the whole range of population sizes from small ones similar to those described here to those which are effectively infinite.

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