GENETIC LOADS AND FITNESS OF POPULATIONS: I. THE EFFECTS OF THE GENE STUBBLE ON FITNESS OF EXPERIMENTAL POPULATIONS OF *DROSOPHILA MELANOGASTER*

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GENETIC loads, or at least their mutational components, reduce the fitness of populations. This conclusion was reached primarily on the basis of mathematical models which take differential but not actual survival into account. That the ecological aspect of the effects of the genetic load has received insufficient attention has been pointed out by several authors. SANGHVI (1963), for example, argued that more information about the effects of the environment on populations is needed before the effects of the genetic load on fitness could be evaluated. BRUES (1964) emphasized the importance of actual survival and pointed out that the elimination of the greatest proportion of offspring due to limiting factors of the environment could hardly be called a load. More work is desirable, therefore, to clarify the problem of the interrelationship of genetic load and fitness of populations.

This paper reports an attempt to experimentally evaluate the effects of the genetic load on the fitness of laboratory populations of Drosophila. Several methods have been proposed to estimate the relative fitness of experimental populations. Two of them are utilized in the present experiments. The first method was originally worked out by BUZZATI-TRAVERSO (1955) and later modified by CARSON (1961) and other investigators. The second was proposed by CLARINGBOLD and BARKER (1961) and modified by STRICKBERGER (1963a). The first method compares the biomass (or number of individuals) maintained or produced in a unit of time by experimental populations; the second employs performances of populations in interspecific competition.

MATERIALS AND METHODS

The gene Stubble (*Sb*) which is a recessive lethal but a phenotypically dominant mutant, was used in the experiments reported below. The flies were derived from the experimental population Stubble Mono 1 (POLIVANOV 1964) in which the gene Stubble had been introduced two years before the present experiments were started. Although Stubble had been reduced to a low frequency, it was still possible to obtain 5 Stubble females and 2 Stubble males. The Stubble females were crossed with 10 wild-type males, and Stubble males were crossed with 5 wild-type females from the same population. The offspring of these flies were utilized as the founder stock

for all experimental populations described in this paper. The populations were kept in a constant temperature room at 25 ± 0.5°C. However, due to mechanical failures the temperature dropped to 23°C or rose to 27°C several times during the course of the experiments. This room had electric lights on for ten or more hours per day, and dim light was on constantly.

Experiment 1: The purpose of this experiment is to compare the relative fitness of Stubble-bearing and Stubble-free populations. Eight populations were started with the F_1 offspring from the original crosses, four of them with Stubble, and four with wild type. Each population initially contained 50 pairs of flies. All the populations were maintained in half-pint milk bottles with approximately equal amounts of SPASSKY's medium to which four drops of Fleischmann's yeast suspension (0.1 g of yeast per 1 cc of distilled water) were added.

All the populations were transferred to fresh bottles four times a week, (on Monday, Wednesday, Friday, and Saturday). When young flies started to emerge from Monday, Wednesday, and Friday bottles, they were collected and stored on unyeasted medium for 1 to 4 days. Mortality of the young flies was usually low and was approximately the same in all populations. Twice a week they were etherized, weighed, and added to the original populations. A sample of about 200–300 flies was weighed separately and then counted in order to estimate the average weight and the total number of flies.

Saturday samples were used only for the estimation of the gene frequency and were not added to the populations. To avoid discrimination against genotypes with slower developmental rates, flies were collected from each bottle as long as they were emerging. Once a week all populations were etherized and weighed. Due to this procedure, the majority of flies received etherization at least twice during their lifetime. The average weight and the total numbers of flies were estimated in the same way as in the case of newly-produced flies. The samples of the adult populations were also used for the estimation of the frequency of the gene Stubble. All the populations were kept on the same shelf, and were arranged in consecutive order. The odd numbers were given to the Stubble-bearing, and the even ones to the wild-type populations. Such seemingly unimportant factors as the location of a population on the shelf apparently had some effects. The more centrally located populations (both Stubble-bearing and Stubble-free) tended to produce greater biomass than the populations located at the ends of the shelf. Since each pair of adjacent populations had the most similar environmental conditions, each pair was regarded as a block and the whole experiment as having a complete-block design.

Experiment 2: This experiment was analogous to the first one but the populations were started with two pairs of flies instead of 50. The flies in this experiment were full sibs, offspring of a single wild-type female and a Stubble male. Both parents were derived from a Stubble stock culture. At the beginning of the experiment, one pair of flies in each population was one day and the other two days old. All flies were unmated before this experiment was started.

Experiment 3: The third experiment was a replication of the second except that the flies were not sibs, but were derived from a mass culture. The founders of these populations, therefore, were raised under more crowded conditions than were those in Experiment 2.

Experiment 4: Two species of Drosophila, namely *Drosophila melanogaster* and *Drosophila simulans*, were used for this experiment. All *D. melanogaster* (both Stubble (*Sb*/+) and wild-type) were the F_2 offspring of the original flies mentioned in the description of Experiment 1. All *D. simulans* were vermilion-eyed mutants. This strain was described by BARKER (1962a). Six populations were started with 50 pairs of *D. melanogaster* and 150 pairs of *D. simulans*. All *D. melanogaster* were unmated and were from 1 to 5 days old at the beginning of the experiment. *D. simulans* were obtained from mass cultures. The age of the flies was unknown. While all *D. simulans* were derived from the same strain and were presumably genetically similar in all populations, populations of *D. melanogaster* were either 100% Stubble or 100% wild type. The numbers C1, C3 and C5 were given to the Stubble-bearing populations and C2, C4, and C6 to the Stubble-free ones. Approximately once per generation all adult flies were removed from the populations (by the use of a vacuum pump), etherized, scored, and then returned to the populations. This method permitted detection of *D. simulans* when they were present at a very low frequency. But the whole procedure was apparently harmful to the flies. Although the great majority of them revived after etherization, the mortality of adults increased in the two days

following the scoring. This fact was probably also responsible for the maintenance of rather small sizes of all populations. All populations were maintained in plastic polyethylene cages (POLIVANOV 1964) in the same room as the populations in Experiment 1.

Experiment 5: After approximately three years Experiment 4 was repeated with some modifications. All flies were derived from the same stocks (as in Experiment 4) which had been maintained during these years in mass cultures. However, since some mutations probably took place during this time, an attempt was made to equalize the genetic background of Stubble-bearing and Stubble-free populations. For this purpose four Stubble virgin females were crossed singly with wild-type males, and one wild-type female with a Stubble male. The populations were started with the F_2 offspring of these flies. Each population received an equal number of flies from each cross. Six populations were started with 30 pairs of *D. melanogaster* and 90 pairs of *D. simulans*. All flies were from 0 to 7 days old. *D. melanogaster* were unmated, while *D. simulans* were derived from mass cultures. In two of these populations the initial frequency of the gene Stubble was 0.50; the other two were free of this gene, while the last two were started with a frequency 0.25 Stubble. The numbers C7 and C9 were given to the populations with a frequency 0.50 Stubble; C8 and C10 to the Stubble-free ones, and, finally C11 and C12 to the populations started with a frequency 0.25 Stubble. In this experiment only males were scored. Populations were maintained in an air-conditioned room with temperature fluctuating between 21 and 26°C.

RESULTS

Experiment 1–The size of populations: Weekly measurements of the biomass of the Stubble-bearing and Stubble-free populations are given in Table 1. The fluctuation in the number of flies was similar in direction but greater in amplitude than the fluctuation in biomass since the average weight of flies was reduced at high density. The average weight of flies in individual samples at low density ranged from 0.75 to 0.88 mg, while at high density it ranged from 0.58 to 0.77 mg.

TABLE 1

Biomass of the populations in grams

Weeks	Stubble-bearing populations				Stubble-free populations			
	1	3	5	7	2	4	6	8
0	0.087	0.086	0.085	0.089	0.087	0.088	0.086	0.087
2	0.129	0.149	0.152	0.160	0.160	0.168	0.202	0.206
3	0.367	0.409	0.649	0.535	0.415	0.414	0.390	0.411
4	0.897	1.366	1.943	1.290	1.000	1.546	1.421	1.199
5	1.579	2.044	2.072	1.782	2.252	2.325	2.084	2.048
6	2.346	2.265	2.343	2.408	2.199	2.502	2.173	2.330
7	2.214	1.952	2.759	2.382	1.903	2.399	2.368	2.381
8	2.295	2.033	2.750	2.792	2.249	2.630	2.653	2.478
10	1.404	0.634	0.971	0.876	2.366	0.492	1.975	0.611
11	1.992	1.831	1.943	1.579	1.658	1.429	1.889	1.969
12	1.004	1.144	1.711	0.843	1.445	1.363	1.764	1.649
13	1.131	1.130	1.219	0.643	1.329	1.036	1.143	1.123
14	1.014	1.089	0.976	0.992	0.983	0.883	1.819	0.836
15	0.917	1.413	1.182	0.866	0.851	1.029	1.048	0.826
16	0.911	1.021	1.029	0.786	0.544	0.742	0.770	0.568
17	1.277	1.297	1.065	0.952	0.520	0.966	1.290	0.713
19	1.047	1.342	1.412	1.283	0.633	1.327	1.071	0.737
20	0.962	1.026	1.042	1.061	0.541	1.501	0.800	0.734

The development of both Stubble and Stubble-free populations proceeded in a rather typical way. An initial period of vary rapid growth was followed by a breakdown and then by fluctuations with decreased amplitudes. Similar patterns of population development have been reported by several investigators, for example, by DOBZHANSKY and PAVLOVSKY (1961). The means of weekly measurements of biomass were very close in both kinds of populations until after the 15th week when biomass means of Stubble-bearing populations became consistently higher than Stubble-free ones (Figure 1). However, there was considerable overlapping in the sizes of both kinds of populations. Comparison of the means of individual populations for the period from the 14th to the 20th week revealed that neither kind nor position on the shelf had sufficiently strong influences to produce statistically significant differences between means of corresponding groups. (Analysis of variance; $P = .95$).

Productivity: The weekly production of biomass is given in Table 2. The means of weekly biomass production of both kinds of populations are presented graphically in Figure 2. These means were very close to each other at the beginning, but after the 14th week, the mean of the Stubble-bearing populations became consistently higher than that of the Stubble-free ones. However, even for this period there was no significant difference between means of both kinds of populations.

As in the case of biomass the peaks of productivity of both kinds of populations were followed by a rapid decrease and then by fluctuations having decreased amplitudes. But the lowering of the level of productivity in both kinds of populations was less pronounced than that of biomass. This fact indicates that the de-

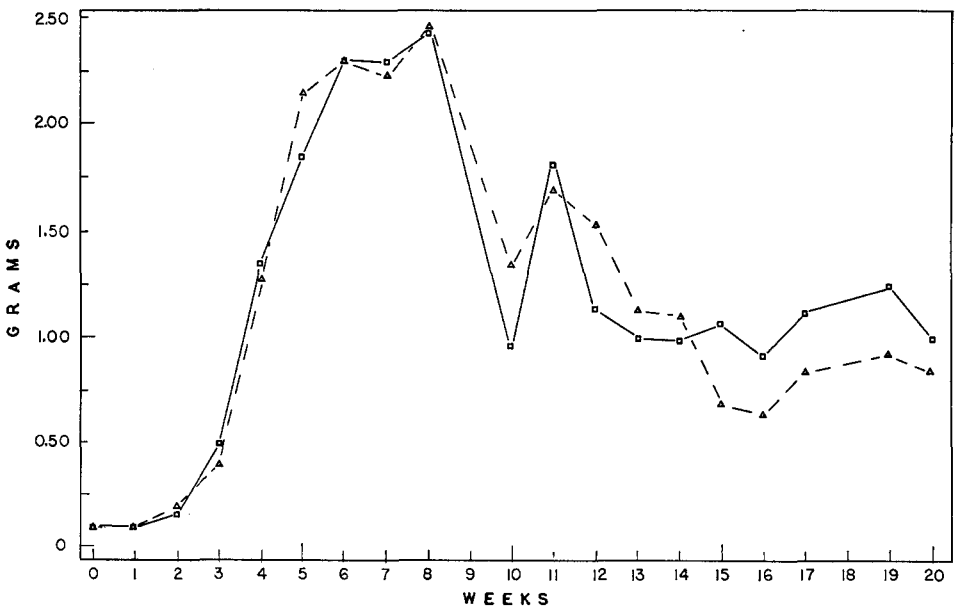

FIGURE 1.—Means of biomasses. Squares: mean of the Stubble-bearing populations; triangles: mean of the Stubble-free populations.

TABLE 2

Biomass production in grams

Weeks	Stubble-bearing populations 1	3	5	7	Stubble-free populations 2	4	6	8
2	0.149	0.173	0.255	0.212	0.263	0.191	0.277	0.284
3	0.543	0.724	1.137	0.769	0.549	0.771	0.606	0.501
4	0.698	1.124	1.443	0.699	1.272	1.490	1.125	1.294
5	1.405	1.564	1.449	1.358	1.658	1.446	1.339	1.344
6	1.521	1.345	1.906	1.744	1.420	1.799	1.531	1.350
7	1.485	1.309	1.665	1.613	1.633	1.660	1.624	1.488
8	2.109	2.036	1.808	2.034	2.092	2.259	1.799	1.918
9	2.682	2.462	2.076	2.633	2.089	2.529	2.319	2.453
10	2.064	1.974	2.129	1.801	1.902	1.937	1.800	2.017
11	2.397	2.252	2.397	1.670	1.748	1.442	1.749	1.875
12	1.713	1.533	2.221	0.645	2.068	1.359	1.902	1.460
13	1.067	1.197	1.225	0.952	1.488	0.949	1.600	1.049
14	1.341	2.058	1.702	1.514	1.419	1.336	2.282	1.041
15	1.238	2.153	1.754	1.477	1.072	1.492	1.912	1.079
16	1.654	1.781	1.846	1.519	0.923	1.201	1.423	0.961
17	1.787	1.676	1.386	1.608	0.818	1.568	1.855	1.210
18	1.168	1.595	1.695	1.418	0.686	1.528	1.292	0.885
19	1.567	1.964	1.974	2.076	0.792	2.074	1.446	1.088
20	1.166	2.014	1.316	1.430	0.853	2.019	1.293	1.043

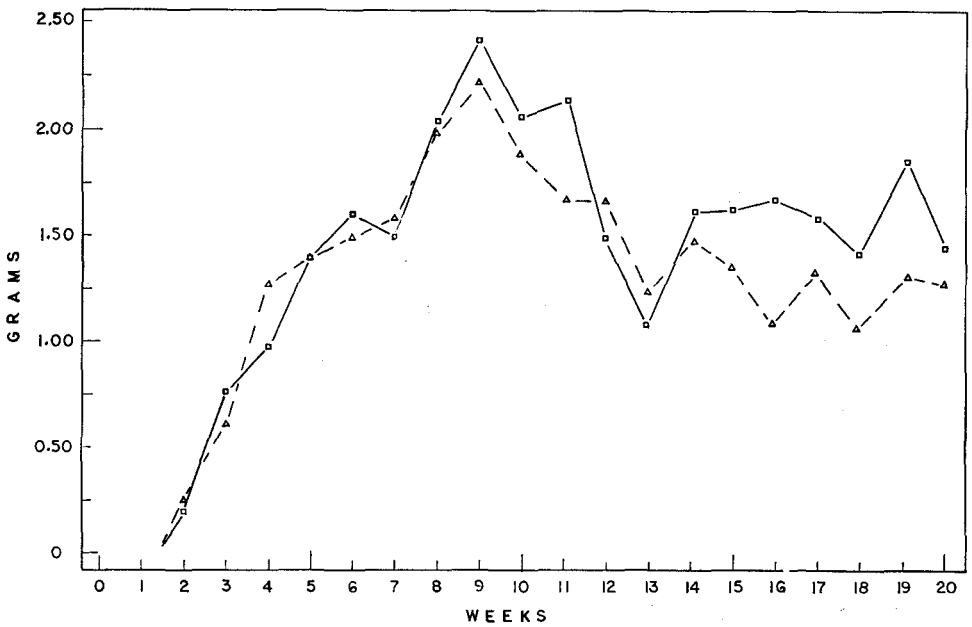

FIGURE 2.—Means of weekly productivities. Squares: mean productivity of the Stubble-bearing populations; triangles: mean productivity of the Stubble-free populations.

crease in the size of populations was caused primarily by the increase in mortality rate, and to a lesser extent by the decrease in productivity.

Frequency of the gene Stubble: The gene Stubble was not balanced by any other lethal factor, and its frequency decreased with time. Figures 3 and 4 show the frequencies of the gene Stubble in the samples from the adult populations and from the Saturday egg samples. These two estimates do not give identical results. Apparently selective forces were slightly more favorable for Stubble heterozygotes in the populations than they were in the less crowded egg samples. According to BARKER (1962b) the generation length of *D. melanogaster* kept in bottles is about 14 days. If this estimate is accepted, then the decrease in the frequencies of Stubble proceeded at a somewhat slower rate than would be expected with a recessive lethal. The majority of points in both estimates lies above the expected curves. However, since no separate estimates of generation length were performed in this experiment, these data could not be used as perfect evidence that the lethal-bearing chromosomes are heterotic with non-Stubble chromosomes.

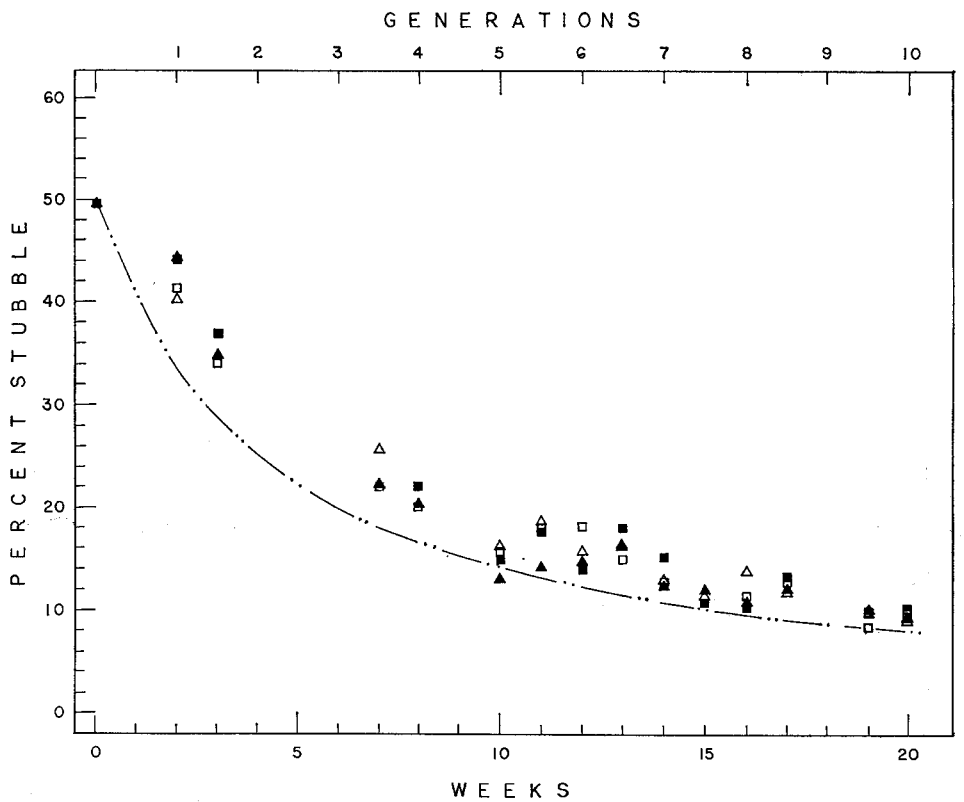

FIGURE 3.—Changes in frequencies of Stubble estimated from samples of adult populations. Solid triangles: population 1; solid squares: population 3; open squares: population 5; open triangles: population 7; broken line separated by two dots: expected curve of elimination of a recessive lethal.

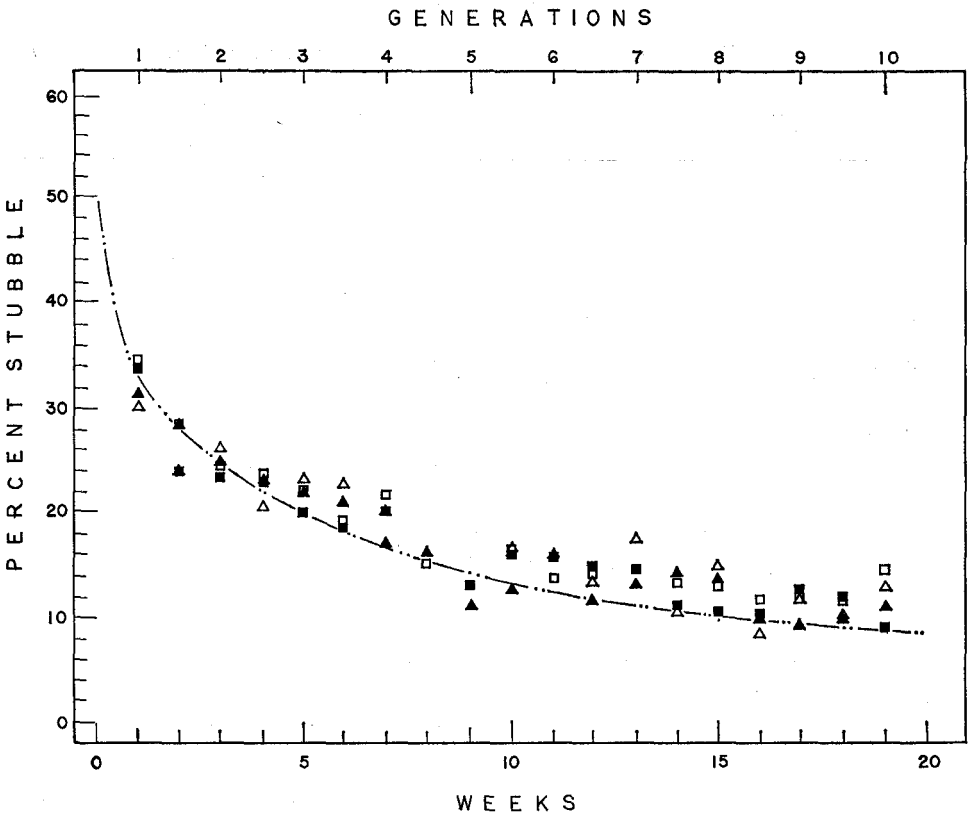

FIGURE 4.—Changes in frequencies of Stubble estimated from egg samples. Symbols as in Figure 3.

Experiments 2 and 3: These two experiments were designed to test the effects of Stubble at a low density and, therefore, the cultures were kept only until the F_2 flies started to emerge. The results of both experiments are presented in Tables 3 and 4. A quarter of the F_1 offspring was eliminated in the Stubble-

TABLE 3

Number of flies in the F_1 populations—Experiment 2 (founders are full sibs)

Stubble-bearing populations		Stubble-free populations	
Population number	Number of flies	Population number	Number of flies
11	884	12	504
13	685	14	326
15	451*	16	415
17	707	18	313
Mean	682	Mean	389.5

* Two cultures of this population were severely affected by some kind of infection. Very few flies emerged in these bottles and all of them were small. The size of flies and the number of emerging adults in the other bottles of this population were normal.

TABLE 4

Number of flies in the F_1 populations—Experiment 3 (founders are derived from a mass culture)

Stubble-bearing populations		Stubble-free populations	
Population number	Number of flies	Population number	Number of flies
21	402	22	351
23	545	24	461
25	574	26	122
27	463	28	724
Mean	496	Mean	414.5

bearing populations due to homozygosity. This loss might have sufficiently reduced the larval density to produce a significantly higher number of surviving adults. (Exp. 2:$\chi^2 = 79.87$, 1 df. Exp. 3:$\chi^2 = 7.29$, 1 df). Such increased number of survivals due to reduction of larval density was reported by LEWONTIN (1955). However, since the flies from the Mono 1 stock had generally very low fecundity (POLIVANOV *et al.* unpublished) and since only two females were present in a given bottle for two days, it is rather unlikely that they would lay enough eggs to produce larval overcrowding. But the exact number of eggs or of first instar larvae is unknown. It is possible to interpret these findings also as a result of heterotic interactions between Stubble-bearing and wild-type chromosomes. But the difference between Stubble-bearing and Stubble-free populations was larger when all founders were full sibs than when founders were derived from a mass culture. Besides, in the latter case one of the Stubble-free populations produced a larger number of flies than Stubble-bearing populations. It is possible, therefore,

TABLE 5

Percent of D. melanogaster *in populations—Experiment 4*

	Stubble-bearing populations					
	C1		C3		C5	
Days	Total	Percent of *D. melanogaster*	Total	Percent of *D. melanogaster*	Total	Percent of *D. melanogaster*
0	400	25.0	400	25.0	400	25.0
26	917	80.3	920	81.5	943	81.5
54	864	96.1	950	94.3	767	95.0
80	649	97.7	722	96.5	653	95.1
108	652	99.2	622	98.4	749	99.5
134	728	99.4	473	98.5	451	99.1
	Stubble-free populations					
	C2		C4		C6	
Days	Total	Percent of *D. melanogaster*	Total	Percent of *D. melanogaster*	Total	Percent of *D. melanogaster*
0	400	25.0	400	25.0	400	25.0
26	882	94.7	1002	92.1	904	90.0
54	698	99.4	686	96.3	873	98.3
80	878	99.8	774	98.7	704	99.3
108	547	100	545	100	620	99.5
134	728	100	631	100	573	100

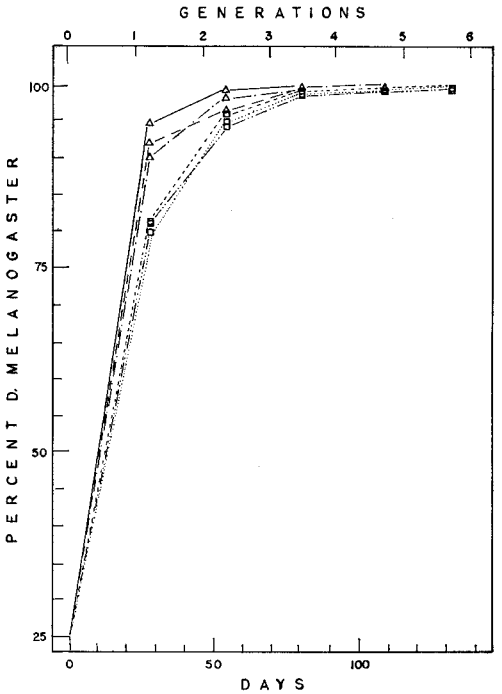

FIGURE 5.—Increase in percent of *Drosophila melanogaster*. Triangles: Stubble-free populations; squares: Stubble-bearing populations.

that heterosis was actually associated with a particular wild-type but not with a Stubble-bearing chromosome.

Experiment 4: The results of this experiment are shown in Table 5 and presented graphically in Figures 5 and 6. The increase in frequency in *D. melanogaster* occurred at somewhat higher rates in the Stubble-free populations than in the Stubble-bearing ones (Figure 5). But in the second generation the difference between replicas of Stubble-free populations was already greater than that between some of the Stubble-free and Stubble-bearing ones. However, there was no overlapping between frequencies of *D. melanogaster* in both kinds of populations. At the termination of the experiment, *D. simulans* was completely eliminated in all Stubble-free populations, while it was still persisting in all Stubble-bearing ones, although its frequencies were reduced to 1.5% or even to fractions of one percent.

The actual numbers of *D. melanogaster* were also higher in Stubble-free than in Stubble-bearing populations. This relationship, however, was observed only in the first generation (Table 5). Both the higher frequencies and the higher numbers of *D. melanogaster* in the Stubble-free populations indicate that they had higher fitness than the Stubble-bearing ones (at least during the first generation). But CLARINGBOLD and BARKER's model for the estimation of relative fitnesses could not be applied in this case, since their model is built on the assumption of

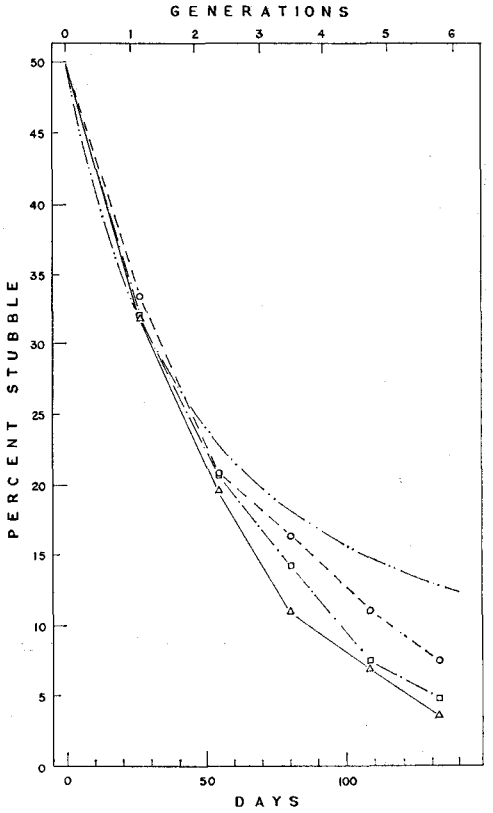

Figure 6.—Changes in frequencies of the gene Stubble. Triangles: population C1; circles: population C3; squares: population C5; broken line separated by two dots: expected curve of elimination of a recessive lethal.

the constancy of adaptive value of the populations in question, while in the present experiment, fitness was changing due to rapid decreases in the frequencies of Stubble. Therefore, the method described by STRICKBERGER (1963a) was used for the comparison of "overall performance" of the populations. This method consists in the estimation of cumulative frequencies of *D. melanogaster* included

TABLE 6

Overall performance of D. melanogaster *in competition with* D. simulans

	Initial frequency of *Sb*		
	0.50	0.25	0
Time to 134 days	C1: 2.254 ± 0.033		C2: 2.411 ± 0.026
	C3: 2.201 ± 0.035		C4: 2.380 ± 0.028
	C5: 2.189 ± 0.035		C6: 2.323 ± 0.029
Time to 75 days	C7: 1.974 ± 0.038	C11: 2.170 ± 0.038	C8: 2.114 ± 0.044
	C9: 2.013 ± 0.041	C12: 2.007 ± 0.041	C10: 2.300 ± 0.038

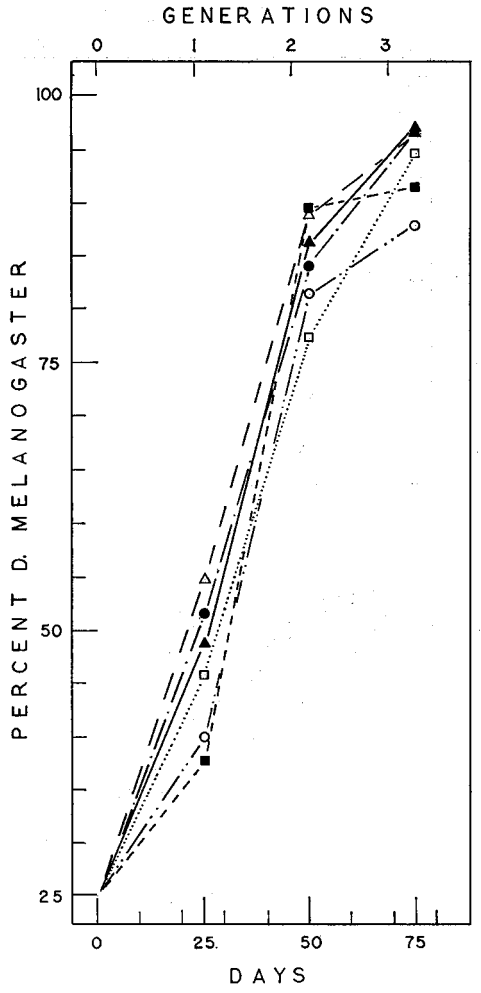

FIGURE 7.—Increase in frequencies of *Drosophila melanogaster* estimated from the male counts. Squares: population started with 0.5 frequency of the gene Stubble; solid squares: population C7; open squares: population C9; circles: populations started with 0.25 frequency of the gene Stubble; solid circles: population C11; open circles: population C12; triangles: stubble-free populations; solid triangles: population C8; open triangles: population C10.

within the area of the frequency polygon. The numerical values of such estimates were termed by STRICKBERGER the "overall performance" of the given population. The results obtained in the present experiment are given in Table 6. As can be seen from this table, the "overall performance" of the Stubble-free populations was higher than that of the Stubble-bearing ones. However, the difference between the lowest Stubble-free and the highest Stubble-bearing populations was barely significant at the 0.05 level of significance. The decreases in the frequencies of Stubble seemed to proceed somewhat faster than expected (Figure 6), suggesting that the Stubble heterozygotes were at a disadvantage. But this conclu-

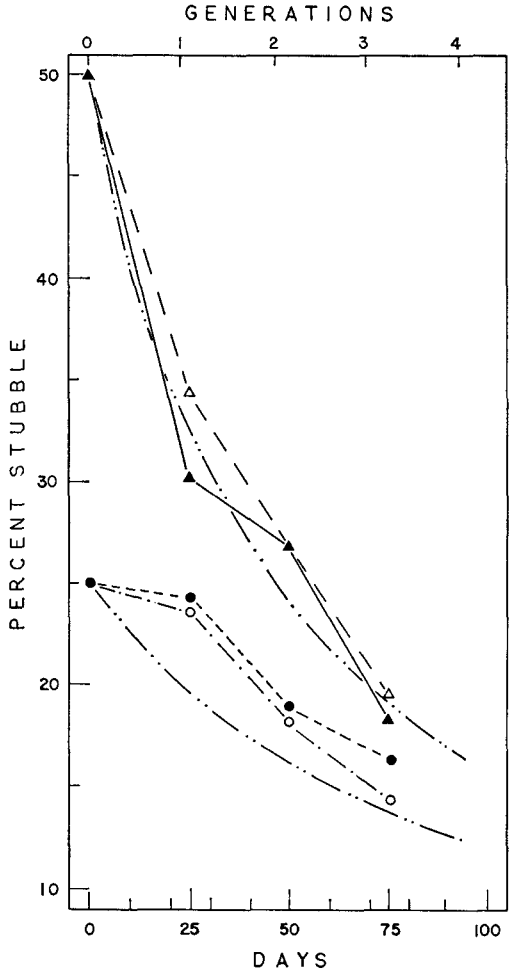

FIGURE 8.—Change in frequencies of the gene Stubble estimated from the male counts. Solid triangles: population C7; open triangles: population C9; solid circles: population C11; open circles: population C12; broken lines separated by two dots: expected curves of elimination of a recessive lethal.

sion could be incorrect; the assumption of a generation length of 23 days (from BARKER 1962b), might not be applicable to the present case.

Experiment 5: The results of this experiment are presented graphically in Figures 7 and 8. The frequency of *D. simulans* rapidly decreased in all the populations, but this process proceeded with a slower rate than in the previous experiment. As in experiment 4, displacement of *D. simulans* in the first generation was somewhat more intense in populations C8 and C10 (Stubble-free) than in C7 and C9 (started with Stubble heterozygotes), while C11 and C12 (started with a frequency 0.25 of Stubble) produced results intermediate between the replicas of both above types (Figure 7). The difference in "overall performance"

of the populations C8 and C9 was barely significant at the 0.05 level, whereas differences between such replicas as C8 and C10, or C11 and C12, were even greater than between C8 and C9. Apparently the gene Stubble had very little effect on the overall fitness of the populations, since divergence between populations, at least between replicas, was most probably attributable to environmental rather than genetical factors.

The frequency of the gene Stubble in this experiment (Figure 8) decreased approximately at the rate expected for a recessive lethal.

DISCUSSION

The ability of a population to maintain a certain size under given environmental conditions was considered by many investigators as a measure of relative fitness. BUZZATI-TRAVERSO (1955), CARSON (1961), DOBZHANSKY and PAVLOVSKY (1961), SMATHERS (1961), CANNON (1963), STRICKBERGER (1963b), AYALA (1965; 1968), and others have shown that genetically different populations maintained, or produced in a unit of time, unequal amounts of biomass or unequal numbers of individuals. In all these cases, however, differences between populations are not reducible to the presence or absence of a single genetic factor but are rather attributable to interactions of many factors. Identification of the particular factors responsible for the production of genetic loads and evaluation of their individual effects on the total fitness of populations is difficult in such cases. More simple systems, as the effect of a single locus, should be used for this purpose. Ideally, two kinds of populations which differ only in the presence or absence of a single deleterious allele should be compared. The material available to the present author which provides a more or less close approximation to the above condition was a stock of Stubble flies derived from an experimental population. In the original population the Stubble chromosome exhibited heterosis but this property was lost after approximately 7 or 8 generations, and the gene Stubble decreased at the rate expected for a recessive lethal.

It is expected that a thorough reshuffling of the genetic material took place in this population, and that the Stubble flies and the wild-type flies differed on the average only in a small segment of the third chromosome around the Stubble locus. In the present experiments the wild-type chromosomes were not tested to determine whether they were carrying newly arisen lethal factors or not. However, it is expected that these factors could not seriously affect the results in this case. The original wild-type strain (SYSP) was inbred by brother-sister mating for 239 generations and was probably nearly isogenic. Therefore, it is highly unlikely that the original wild-type third chromosomes carried any lethals in them. Further, if the average mutation rate to lethals is approximately 0.64 percent per third chromosome per generation (WALLACE 1968), and if there is no loss of new mutants due to accidental drift, and if there is no selection against them in the heterozygous state, then the total probability that any wild-type chromosome would carry at least one lethal factor after 40 generations is 0.26. Forty is the number of generations which should have taken place from the start of the population Stubble Mono 1 to the beginning of the present experiment, if

CROW's estimation of generation length is accepted (CROW *et al.* 1967). According to BARKER (1962b) this period of time should comprise only about 30 generations. All Stubble flies received their wild-type chromosomes from the wild-type parents, and these chromosomes must have been equally distributed among Stubble and wild-type flies. All wild-type flies received their chromosomes from the Stubble and wild-type parents. Since there were 7 original Stubble progenitors, there were 7 wild-type chromosomes which were introduced into Stubble-free, but not into Stubble-bearing populations. The average frequency of each of these chromosomes was 1/14 at the beginning of the experiment. If all these data are taken into consideration, then it could be expected that approximately 8 or 9 out of 1,000 zygotes would be eliminated due to new lethals in Stubble-free but not in Stubble-bearing populations. However, the loss of lethals due to accidental drift and due to selection must have taken place, and the loss of zygotes due to lethality in Stubble-free populations must have been considerably smaller. Besides, under the conditions of an experiment where approximately 99% of all zygotes die due to the limiting factors of the environment (BARKER 1967), the loss of even 9 out of 1,000 zygotes would be experimentally undetectable and the Stubble-free populations should not noticeably suffer from the presence of these new lethals. Apparently the newly-arisen lethals did not affect the Stubble-bearing populations either. The gene Stubble was decreasing at approximately the expected rate and no indication was found of the formation of balanced lethal systems. All these arguments are probably superfluous. However, since some investigators raised objections that the results of similar experiments cannot be considered as valid unless all chromosomes were tested for the presence of lethals, the author decided to include them in this paper.

NICHOLSON (1954) has shown that the size of a population is largely controlled by the interaction of density-dependent factors. If one of these factors that tends to reduce the size of a population–for example, predation, is intensified, others are automatically relaxed, allowing the population to maintain its stability. Lethal genes could also induce such density-governed reactions, since in a certain respect their effects are similar to the effects of predation. If this is really so, then such density-governed reactions may completely mask the effects of the genetic load produced by lethal genes. Elimination of one class of homozygotes would increase the amount of available food, which in turn would increase the survival of other genotypes.

The results of Experiment 1 are in rather good agreement with the above hypothesis. All populations were able to produce and maintain approximately the same biomass. Despite the fact that some inequalities have been observed among the populations, no significant difference has been found between them. This fact indicates that the compensatory reactions took place in the Stubble-bearing populations. However, SPASSKY *et al.* (1960) have not observed such compensation in the cultures of *Drosophila pseudoobscura* in which the viability of homozygotes was deficient. But the possibility cannot be excluded that these cultures were not overcrowded enough to exhibit the full effect of density-governed reactions. Consequently, SPASSKY's findings are not necessarily in contradiction with the present results. The results of the competition experiments,

however, indicate somewhat lower fitness of populations started with a frequency .50 Stubble. The difference between them and the Stubble-free populations was barely significant in both the 4th and 5th experiments. Moreover, the populations started with a frequency 0.25 Stubble were not significantly different from the Stubble-free ones. These results support in general the hypothesis developed above, although the whole situation in populations containing two species must have been more complex than in those containing only one. If elimination of Stubble homozygotes in the monospecific populations led to the increase in survival of viable genotypes of *D. melanogaster*, then in the competition experiments similar compensatory reactions permitted a greater survival of *D. simulans*. Consequently, it is understandable why the effects of the genetic loads were not noticeable in the monospecific but were detectable in dispecific populations. Some investigators, such as MATHER (1961), however, expressed an opinion that competitive ability does not necessarily reflect overall fitness. But whether we accept the results obtained from the biomass measurements in monospecific populations or from "overall performances" of populations under interspecific competition as the more reliable, each of them indicates that the presence of Stubble reduces the fitness of populations only when it is found in a very high frequency. In other words, populations can carry considerable amounts of the genetic load produced by such genes as Stubble without a noticeable loss of their overall fitness. The absence of the reduction of fitness must be attributable to the compensatory reactions of populations, but it is difficult to decide on the basis of the present work whether these compensatory reactions were attributable only to interactions of density-dependent factors, or to other forces such as heterosis and mutual facilitation among genotypes. The results of Experiments 2 and 3, and the higher productivity of Stubble-bearing populations at equilibrium in Experiment 1 strongly suggest heterosis. However, the decrease in the frequencies of Stubble in the different populations does not give conclusive support for this hypothesis.

It is more than probable that compensatory reactions in the populations are very complex in their nature and depend on the interactions of different kinds of mechanisms. An attempt to decide whether the compensatory reactions depend primarily on density-dependent factors or on such factors as heterosis will be given in following papers.

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SUMMARY

An attempt has been made to compare the relative fitnesses of experimental populations which differed initially in the known amount of genetic load produced by the recessive lethal gene, Stubble. The populations were started with frequencies of 0.50 and 0.25 Stubble, or they were free of this gene. All flies were derived from the same stock, and all populations differed on the average only in the frequencies of a short segment of the third chromosome containing the gene,

Stubble. Estimation of relative fitnesses was carried out on the basis of the abilities of populations to produce or maintain biomass, and on the performances of populations under interspecific competition with *Drosophila simulans*. The means of productivity or ability to maintain biomass were not significantly different in Stubble-bearing and Stubble-free populations. The results of competition experiments indicate that populations started with a frequency 0.5 Stubble had somewhat lower fitness than the Stubble-free ones. The difference between populations, however, was barely significant. It was suggested that populations in a limited environment have strong compensatory reactions and, due to their interactions, may carry considerable amounts of genetic load without losing overall fitness.

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