GENETIC VARIATION AND GENETIC LOAD DUE TO THE MALE REPRODUCTIVE COMPONENT OF FITNESS IN DROSOPHILA

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ABSTRACT

The genetic variation and genetic load due to virility, the male reproductive component of fitness, was measured in *Drosophila melanogaster* and *D. pseudoobscura* using males homozygous and heterozygous for the second chromosome of each species. Virility was determined in a female-choice, male mating competition experiment where both mating propensity and fertility were taken into account.——The mean virility of the homozygous *D. melanogaster* males relative to the heterozygous males was 0.50; the relative mean virility of the quasinormal homozygotes was 0.56. The mean virility of the homozygous *D. pseudoobscura* males relative to the heterozygous males was 0.70; the relative mean virility of the nonsterile homozygotes was 0.72, and of the quasinormal homozygotes, 0.68.——Depending on the species and chromosome sampled, fertile homozygous males had a mean virility 15 to 50% lower than the mean viability of individuals homozygous for a chromosome with quasinormal viability. The genetic load due to virility was also greater than that due to the female reproductive component. This higher level of hidden genetic variation (or genetic load) indicates that the results of PROUT (1971a, b) and BUNDGAARD and CHRISTIANSEN (1972), where the virility component of fitness dominated the dynamics of an artificial polymorphism, may be more general and that virility may dominate the dynamics of natural polymorphisms as well.

WITH the increased attention paid to components of fitness in natural and experimental populations of Drosophila, it has become apparent that the male reproductive component is one of the more important components of fitness. "Virility" (PROUT 1971a), as a component of fitness, deals with differences in physiological and behavioral abilities of males, as well as actual performance under competitive conditions. Excellent reviews summarize the work with Drosophila on courtship (SPIETH 1968), mating propensity (SPIESS 1970), mating competition (PETIT and EHRMAN 1969), reproductive biology (LEFEVRE and JONSSON 1962; FOWLER 1973) and sperm competition (PARKER 1970). Here, the concern is the magnitude of virility effects in relation to the other components of fitness.

A number of techniques have been developed to estimate fitnesses at various stages in the life cycle. The methods of ANDERSON (1969), POLIVANOV and ANDERSON (1969), and SVED and AYALA (1970) were used to estimate fitnesses in

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continuous-generation experimental populations with two viable genotypes. They estimated pre-adult and adult fitnesses; by necessity, however, the male and female components were lumped together. Results from studies on Drosophila (POLIVANOV and ANDERSON 1969; SVED and AYALA 1970; SVED 1971; TRACEY and AYALA 1974) have generally demonstrated that both pre-adult and adult components are important in estimating the net fitness of the chromosomes studied.

PROUT (1971a, b) and BUNDGAARD and CHRISTIANSEN (1972) used a more analytical approach with discrete generations and were able to estimate pre-adult, adult male and adult female fitnesses in an experimental population with three discernible genotypes. They found not only that the adult components were important, but also that virility dominated the dynamics of the artificial polymorphism studied.

Studies of natural chromosomal polymorphisms were carried out to detect selective differences among males with different chromosomes. SPIESS and his co-workers (SPIESS and LANGER 1961, 1964a, b; SPIESS, LANGER and SPIESS 1966) looked at mating propensity differences between males homozygous and heterozygous for chromosome *3* inversions in *D. pseudoobscura* and *D. persimilis*. They found, in general, that the fitness of homozygotes was correlated with the frequency of the chromosome in nature and that heterozygotes showed heterosis. ANDERSON *et al.* (1979) found evidence for virility selection occurring in nature by comparing the frequency of inversions among males and among the offspring of females in the same population of *D. pseudoobscura*.

The study reported here used a female choice or male mating competition experiment to determine the virility of males from extracted chromosome lines. The lines used were established using the same scheme as DOBZHANSKY, HOLZ and SPASSKY (1942) and MARINKOVIĆ (1976b) used for *D. pseudoobscura* and as TEMIN (1966) used for *D. melanogaster*. Chromosome *2* was chosen for both species because of the large amount of fitness data in the literature pertaining to the other components of fitness. The methods of estimating virility were similar to those of SPIESS and LANGER (1961), except that genetic markers were used to determine which type of male mated with each female, and the progeny of each female were assayed, rather than dissecting the female. This procedure took into account both behavioral and physiological effects. Thus, the "mating propensity" of SPIESS, which did not take into account whether males were fertile, was combined with the "fertility" of TEMIN (1966), where males were not in competition with other males for mates.

MATERIALS AND METHODS

Drosophila melanogaster: The 27 chromosome *2* nonlethal homozygous lines of *D. melanogaster* used in this study were extracted by R. W. MARKS and include those of MARKS (in preparation). The *SM5* balancer was used to extract the chromosomes and was segregating in most of the lines. The extraction technique resulted in lines homozygous for one wild chromosome *2* (40% of the genome) and for the *Y* chromosome of the wild male. It also replaced the wild *X* and about 75% of the wild chromosomes *3* and *4* with ones in the extraction stock. Males heterozygous for two second chromosomes were produced by crossing virgin females from one line

with males from the next line, in numerical order, except that males from the last line in order were crossed with females from the first. The control line against which all the other lines were competed was a standard laboratory stock and contained the chromosome *2* recessive marker *st* (scarlet eyes).

All lines were maintained in half-pint milk bottles on cornmeal-agar-molasses-propionic acid medium at 25°. Females were allowed to lay eggs for 4 days and then were removed. Generally, only those flies that eclosed on the 10th through 13th day were used.

The female-choice mating experiments were done with 20 5-day-old virgin *st* females; ten 70 to 76 hr (three-day)-old virgin *st* males; and ten 46 to 52 hr (two-day)-old virgin experimental males. All 40 flies were placed in a mating chamber without etherization. The mating chambers, suggested by HERMAN SPIETH, consisted of an 8 dram shell vial (25 mm diameter and 94 mm length) with a damp cylinder of sponge in the bottom and plugged with rayon. After 3 hr in the chamber, the parent flies were etherized, recounted, and the females placed individually in food vials. Later, the progeny in each vial were scored as to the type of male with which the female had mated: *st* progeny implied a *st* male, and wild-type progeny implied an experimental male.

Drosophila pseudoobscura: Forty-six lines of *D. pseudoobscura* homozygous for a nonlethal chromosome *2* were established from collections in San Diego, California, by D. G. FUTCH (F01 to F30); Monterey Peninsula Winery, Monterey, California by R. W. MARKS (M01 to M07); and Gundlach-Bundschu Vineyards, Vineburg, Sonoma County, California (G01 to G45). The chromosomes were extracted from wild males or sons of wild females using *Ba upt bx gl (Inv) / Δ ubx gl²* by the usual methods (DOBZHANSKY, HOLZ and SPASSKY 1942; MARINKOVIĆ 1967b). The technique results in lines homozygous for one of the second chrmosomes (20% of the genome) and with the *Y* chromosome of the wild male. It also replaces the wild *X* and 75% of the wild chromosomes *3*, *4* and *5* with ones in the extraction stock. The fertile lines from Gundlach-Bundschu were maintained as homozygotes, while the balancer was allowed to segregate in the other lines. Heterozygous males were produced by crossing two randomly chosen lines. The control line used contained the chromosome *3* marker *or* (orange eyes).

Note that the "second" chromosome was used in both species. Chromosome *2* of *D. pseudoobscura* is homologous to the right arm of chromosome *3* of *D. melanogaster*, while chromosome *2* of *D. melangaster* is equivalent to a fusion of chromosomes *3* and *4* of *D. pseudoobscura* (STURTEVANT and TAN 1937).

All lines were maintained in the same manner as were the *D. melanogaster* lines, except that they were kept at 22°, and the adults were allowed to lay eggs 5 to 10 days depending on how many larvae were apparent on the fifth day, in an attempt to keep all stocks at a constant density. In the lines with the balancer, all homozygous males were removed each generation 5 days after they started emerging. In the lines without the balancer, males were collected at five-day intervals as needed.

Matings took place at 25° in the same type of chamber as *D. melanogaster*, except that a 5% sucrose solution was used to moisten the sponge. Twenty 5- to 7-day-old virgin *or* females; ten 5- to 6-day old *or* males; and ten 5- to 10-day-old experimental males were placed in the vials without etherization. After 24 hr, the flies were etherized, recounted and the females placed individually in food vials. Later, the offspring in the vials were scored to indicate the type of male with which the female had mated.

Fitness estimation: The virility of the experimental males relative to the control males was estimated using the method of HALDANE (1956). The virility, V, for each experiment or chamber is $V = [b/(a+1)] \cdot [c/d]$, where a is the number of females with *st* or *or* offspring, b is the number of females with wild-type offspring, c is the number of *st* or *or* males, and d is the number of experimental males. The $[c/d]$ term is necessary to compensate for occasional loss of flies when the experiments were set up. HALDANE showed that his estimator was almost unbiased, so that the mean virility, $\overline{V}$, with its associated variance, is distributed around $\hat{V} = [\Sigma b/\Sigma a] \cdot [\Sigma c/\Sigma d]$, which is the lumped estimate for a given line and has no empirical variance.

The Bartlett-Box test was performed on all the virility data to test for homogeneity of vari-

ances before the one-way analysis of variance. The test was also done on the data following the transformation $P = arcsine \sqrt{V/(V+1)}$. Based on the results of the Bartlett-Box tests, the one-way analysis of variance for the *D. melanogaster* homozygotes reported here was done on the virility data directly, while the one-way ANOVA for the *D. melanogaster* heterozygotes and the all *D. pseudoobscura* data were done on transformed virilities.

The SPSS (Statistical Package for the Social Sciences) modified least-significant-difference (LSD) contrast procedure was used to determine which lines were different from the main body of lines at the $p = 0.05$ level. The central group of lines will be referred to as the quasinormal lines. This procedure, like the standard LSD procedure, used the t distribution to calculate ranges, but the LSD is calculated in a more conservative way. Thus, the modified LSD procedure is more conservative than a paired t-test procedure like LSD, but it is not as conservative as the SCHEFFÉ procedure, which takes the total variance into account.

RESULTS

Drosophila melanogaster: The virility estimates for the 27 homozygous *D. melanogaster* lines relative to the *st* control line are shown in Table 1. The mean over all lines was 0.422 ± 0.037, with a standard deviation of 0.193. One-way analysis of variance using V showed that there was significant heterogeneity between the line means [$F(26,243) = 12.39$; $p<0.001$]. The modified LSD procedure results indicated that the two sterile lines (4 and 41) and the partially sterile line (29), were significantly different from the majority of lines. Without these three lines, the mean virility of the quasinormals was 0.473 ± 0.026.

The virility estimates for the 27 heterozygous *D. melanogaster* crosses relative to the *st* control line are shown in Table 2. The mean for all crosses was 0.839 ± 0.030, with a standard deviation of 0.156. One-way ANOVA using V transformed to P showed that there was significant heterogeneity between cross means

TABLE 1

Virility estimates for the 27 Drosophila melanogaster *homozygous lines relative to the* st *control line*

Line	Virility	Line	Virility
1	0.505 ± 0.051	23	0.407 ± 0.086
2	0.302 ± 0.053	25	0.525 ± 0.051
4	0.000 ± 0.000	27	0.339 ± 0.048
6	0.412 ± 0.063	29	0.059 ± 0.024
7	0.455 ± 0.049	30	0.479 ± 0.071
8	0.372 ± 0.037	32	0.650 ± 0.068
9	0.364 ± 0.065	33	0.341 ± 0.024
10	0.519 ± 0.040	34	0.645 ± 0.043
11	0.285 ± 0.039	37	0.589 ± 0.067
14	0.437 ± 0.061	38	0.586 ± 0.061
15	0.549 ± 0.045	39	0.189 ± 0.035
16	0.658 ± 0.073	41	0.000 ± 0.000
17	0.380 ± 0.061		
21	0.732 ± 0.056	Mean	0.422 ± 0.037
22	0.533 ± 0.086		

All lines had ten replicates.

TABLE 2

Virility estimates for the 27 Drosophila melanogaster *heterozygous crosses relative to the* st *control line*

Cross†	Virility	Cross†	Virility
0102	0.885 ± 0.108	2325	0.885 ± 0.094
0204	0.806 ± 0.099	2527	0.651 ± 0.081
0406	0.804 ± 0.124	2729	0.788 ± 0.051
0607	0.706 ± 0.062	2930	0.871 ± 0.109
0708	0.662 ± 0.045	3032	0.865 ± 0.091
0809	0.633 ± 0.054	3233	1.158 ± 0.087
0910	0.816 ± 0.035	3334	1.133 ± 0.155
1011	0.659 ± 0.067	3437	0.875 ± 0.061
1114	0.710 ± 0.065	3738	0.871 ± 0.080
1415	1.032 ± 0.073	3839	0.808 ± 0.065
1516	1.174 ± 0.216	3941	0.788 ± 0.044
1617	0.675 ± 0.091	4101	1.013 ± 0.055
1721	0.944 ± 0.113		
2122	0.655 ± 0.058	Mean	0.839 ± 0.030
2223	0.789 ± 0.085		

All lines had ten replicates.
† The first two digits refer to the line number of the female parent of the males tested and the second two digits to the male parent.

[$F(26,243) = 2.97$; $p<0.001$.] The modified LSD procedure indicated that none of the lines were significantly different from the majority of lines.

Wilcoxon's rank-sum test was used to test whether the virility of homozygote lines was significantly different from the virility of the heterozygote crosses. This test was used because it does not make any assumptions about the distribution of the two samples. Although the heterozygote distribution appears to be normal, the homozygote distribution clearly was not normal. The test showed that the homozygotes and the heterozygotes came from the same "population" with a probability of less than 0.001 [$W_n(27,27) = 391$]. In summary, the mean virility for the homozygote lines relative to the heterozygote crosses was 0.503; it was 0.563 with the sterile and partially sterile lines removed.

The heterozygote crosses were done systematically so that parent-offspring regression could be done using the virility estimates. After removing the data for the sterile and partially sterile lines, the regression of the mid-parent virility (mean virility of the maternal line and paternal line) on the virility of the heterozygote cross was not significant [$F\ (1,19) = 3.52$, $p > 0.05$], nor was the regression of the maternal line virility on the heterozygote cross virility [$F(1,22) = 0.007$, $p > 0.9$]. The regression of the paternal line virility on the heterozygote virility was significant [$F(1,22) = 6.63$, $p < 0.025$]. The slope of the regression line was 0.594 ± 0.005. Although these results cannot be used to estimate heritabilities by the usual methods, they do indicate that there was a strong paternal effect. This could be due, in part, to the *Y* chromosome. However, the large load found among the homozygotes that are identical to the heterozygotes with respect to the *Y* indicates that there is a major effect due to chromosome *2*.

Regression of the virility estimates on the component data of MARKS (in preparation) where the lines were the same was done to determine whether there was a correlation between virility and other components of fitness. MARKS measured the survival and development time from newly hatched larva to adult and adult female weight at six larval densities for 20 lines, 18 of which also were used in this study. Regression of virility on survival at a density of 40 larvae per vial was not significant [$F(1,16) = 1.98$; $p > 0.1$], nor were similar regressions on development time [$F(1,16) = 0.07$; $p > 0.7$] and female weight [$F(1,16) = 1.73$; $p > 0.2$]. MARKS also found no correlations among the three components in his study. The regression of virility on female weight was of particular interest because of the correlation between female weight and female fecundity (BARKER and PODGER 1970). This lack of measurable correlation between the adult components, as well as between the adult and pre-adult components, is consistent with the work of others on random samples of structurally normal chromosomes (DOBZHANSKY, HOLZ and SPASSKY 1942; MARINKOVIĆ 1967a, b) and means that the fitnesses found for each component can be assumed to be independent.

Drosophila pseudoobscura: The virility estimates for the 46 homozygous *D. pseudoobscura* lines relative to the *or* control line are shown in Table 3. The

TABLE 3

Virility estimates for the 46 Drosophila pseudoobscura *homozygous lines relative to the* or *control line*

Line	Replicates	Virility	Line	Replicates	Virility
F01	8	0.769 ± 0.158	G14	10	0.975 ± 0.179
F03	11	0.489 ± 0.127	G15	10	0.392 ± 0.066
F05	10	0.570 ± 0.073	G16	10	0.726 ± 0.096
F08	10	0.625 ± 0.144	G17	10	0.555 ± 0.082
F09	11	0.698 ± 0.128	G18	10	0.332 ± 0.074
F11	11	0.520 ± 0.116	G20	10	0.703 ± 0.142
F12	11	0.425 ± 0.119	G21	6	0.329 ± 0.078
F16	12	0.801 ± 0.139	G22	7	0.565 ± 0.043
F17	10	0.989 ± 0.182	G25	10	0.607 ± 0.083
F18	20	0.411 ± 0.067	G26	10	0.437 ± 0.070
F20	10	0.652 ± 0.098	G27	10	0.487 ± 0.097
F22	10	0.096 ± 0.019	G28	10	0.978 ± 0.126
F23	10	1.514 ± 0.241	G34	10	0.556 ± 0.099
F24	10	0.410 ± 0.088	G36	10	0.651 ± 0.108
F25	11	0.640 ± 0.072	G42	10	0.692 ± 0.090
F26	10	0.893 ± 0.120	G44	6	0.346 ± 0.073
F30	11	0.536 ± 0.095	G45	10	0.403 ± 0.060
G01	10	0.442 ± 0.073	M01	11	1.491 ± 0.521
G03	10	0.449 ± 0.080	M03	11	0.445 ± 0.077
G06	10	0.576 ± 0.248	M05	9	0.265 ± 0.053
G08	10	0.530 ± 0.081	M06	11	0.663 ± 0.168
G09	10	0.033 ± 0.017	M07	11	0.889 ± 0.208
G10	10	0.238 ± 0.051			
G12	10	0.478 ± 0.078	Mean		0.593 ± 0.042

mean for all lines was 0.593 ± 0.042, with a standard deviation of 0.228. One-way ANOVA using the virilities transformed to P showed that there was significant heterogeneity between line means [$F(45,422) = 7.22$; $p < 0.01$].

The modified LSD contrast procedure results indicated that the two partial steriles, lines F22 and G09, were significantly different from the majority of lines. In fact, these lines initially may have been completely sterile, since the *Ba* balancer is not as good as the *D. melanogaster SM5* balancer. The mean virility of the nonsteriles was 0.617 ± 0.041. The other line that stands out in the LSD analysis is F23. It is effectively supervirile. The same procedure done using untransformed virilities indicates that both lines F23 and M01 were significantly different and supervirile. The mean virility of the quasinormals (lines F22, F23, G09, and M01 removed) was 0.575 ± 0.030.

The virility estimates of the 23 heterozygous crosses relative to the *or* control line are shown in Table 4. The mean over all crosses was 0.851 ± 0.040, with a standard deviation of 0.191. One-way ANOVA using the transformed virilities showed that there was significant heterogeneity between the means for each cross [$F(22,225) = 1.96$; $p = 0.008$]. However, there was not enough heterogeneity for the modified LSD procedure to find any line significantly different from another.

Wilcoxon's rank-sum test was used to test whether the sample of homozygous lines was significantly different from the heterozygous crosses. The test showed that they came from the same population with a probability of less than 0.001 [$W_n(23,46) = 1134$]. In summary, the mean virility relative to the heterozygotes for all the homozygotes was 0.696, for the nonsteriles 0.725, and for the quasinormals 0.675.

TABLE 4

Virility estimates for the 23 Drosophila pseudoobscura *heterozygous crosses relative to the* or *control line*

Cross*	Replicates	Virility	Cross*	Replicates	Virility
F0317	16	1.142 ± 0.196	G0622	10	0.811 ± 0.137
F0509	12	1.113 ± 0.215	G0910	10	1.126 ± 0.162
F1112	16	0.719 ± 0.126	G1016	10	0.756 ± 0.082
F1618	18	0.684 ± 0.081	G1214	10	0.807 ± 0.193
F1623	10	0.918 ± 0.191	G1516	10	1.115 ± 0.160
F1820	9	0.559 ± 0.121	G2028	8	0.854 ± 0.168
F2025	8	0.812 ± 0.115	G2223	10	0.955 ± 0.261
F2122	6	0.892 ± 0.225	G2526	9	1.077 ± 0.134
F2130	15	0.886 ± 0.133	G2527	11	0.974 ± 0.158
F2325	10	0.550 ± 0.107	G2728	10	0.821 ± 0.087
G0103	10	0.458 ± 0.068	G3334	10	0.693 ± 0.082
G0608	10	0.861 ± 0.059			
			Mean		0.851 ± 0.040

* The first two and second two digits refer to the line numbers of the parents of the males tested.

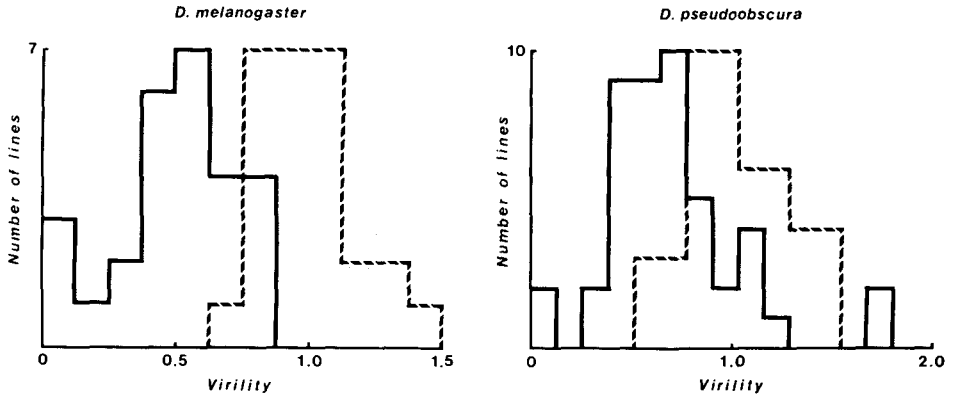

FIGURE 1.—Virility distributions of the lines homozygous (solid line) and heterozygous (dashed line) for chromosome 2 of *Drosophila melanogaster* and *D. pseudoobscura*. The virilities have been scaled so that the mean of the heterozygotes is 1. The histogram interval for the *D. pseudobscura* heterozygotes is twice as large as for the homozygotes so as to account for the smaller sample size.

Comparison of D. melanogaster *and D. pseudoobscura*: The *D. melanogaster* homozygous chromosome lines used in this study had a lower mean virility relaitve to the heterozygotes than did the homozygous *D. pseudoobscura* lines. This difference can be seen in Figure 1, where the distributions of the virilities are given. Although the comparison is between very different species and the chromosomes themselves are not homologous, the decrease found for *D. melanogaster* would be expected, based on the data for *D. pseudoobscura* under the assumptions of multiplicative fitnesses and no chromosome-arm fitness interactions. *D. melanogaster*, with twice as much of the genome homozygous, has a homozygous fitness approximately the square of the homozygous fitness found for *D. pseudoobscura* when all the chromosome lines, and when only the nonsterile chromosome lines, are considered.

DISCUSSION

The amount of hidden genetic variation and genetic load in chromosomes from natural populations of Drosophila has now been ascertained for the major components of fitness: viability (egg to adult survival), female fertility and fecundity, and virility (male fertility and mating propensity). Studies have also been done on other fitness-related aspects of the life cycle, such as development rate. Taken together, the fitness distributions of each component are beginning to give a clear picture of fitness or genetic load effects during the various stages of the life cycle.

The distributions of chromosomal fitnesses give a similar qualitative picture for each of the fitness components. The heterozygote fitnesses, where each heterozygous cross mimics a wild individual, are generally normally distributed. The mean of this distribution is assigned the fitness value of 1.0. The distributions of homozygous fitnesses are generally bimodal. Previous authors have tended

arbitrarily to divide up the distributions into four classes. The four classes are also noted following a statistical analysis like the one used here, although the boundaries may be different. One class contains the chromosomes with zero homozygous fitness: the lethals and steriles. The second class, the quasinormals, contains the majority of chromosomes; they are approximately normally distributed with a mean less than that of the heterozygotes and a variance somewhat larger than the heterozygote variance. It is observed that a number of nonlethal or nonsterile chromosomes have fitnesses significantly removed from the quasinormals. The chromosomes that fall between the lethal or sterile class and the quasinormals constitute the third class: the semilethals and semisteriles. The fourth class contains a relatively small number of chromosomes that could be considered supervital or supervirile; they have a fitness higher than that expected of a quasinormal chromosome.

Each component of fitness has a different, though characteristic, proportion of chromosomes falling into each class. In *D. pseudoobscura*, the mean homozygote virility is similar to the mean viability as found by DOBZHANSKY and SPASSKY (1953), DOBZHANSKY, SPASSKY and TIDWELL (1963) and MARINKOVIĆ (1967a). The fitness distributions for each component, however, are very different. They found that 13% of all chromosomes are homozygous lethal, while 17% are semilethal and 70% are quasinormal. For the virility component, only 4 to 8% are sterile or semisterile (the 8% sterility found by DOBZHANSKY and SPASSKY (1953) is not significantly different from the results reported here), while 90% are quasinormal. A result of the different distributions of fitness is that, in an experiment where only quasinormal chromosomes are considered, the expected homozygous virility is 0.68, while the expected homozygous viability is 0.85. If the supervirile lines are included, the expected homozygous virility is 0.73. It should be pointed out that these fitness values are, to some extent, dependent on experimental conditions. MARINKOVIĆ (1971b) used a different technique to measure viability from that used in the above studies. He found essentially the same fitness distribution, execpt that the mean of the quasinormal homozygotes was reduced to 0.74.

In *D. melanogaster*, the picture is similar to that in *D. pseudoobscura*. GREENBERG and CROW (1960) and TEMIN (1966) found a mean relative homozygous viability of 0.65 and a mean of the quasinormals of 0.86. The virilities reported here are 0.50 and 0.56 for the two classes, respectively.

The female reproductive component of fitness in Drosophila has not been studied in sufficient detail in one species, so that the results of TEMIN (1966) for *D. melanogaster*, and DOBZHANSKY and SPASSKY (1953) and MARINKOVIĆ (1967a) for *D. pseudoobscura* need to be considered together. TEMIN (1966) found that 4.2% of *D. melanogaster* homozygous second chromosomes produce physiologically sterile females, while the rest of the chromosomes produce females, all of which could be considered fertile. Similarly, DOBZHANSKY and SPASSKY (1953) found 10.6% female steriles for chromosome *2* of *D. pseudoobscura*. Fecundity or egg production rate of females was measured by MARIN-

KOVIĆ (1967a). He found that all females laid eggs, whether or not they were fertile. In a sense, they were all quasinormal and had a mean homozygous fitness of 0.79. Thus, the female reproductive component has a proportion of steriles similar to the male component, but has an expected quasinormal fitness similar to that found for the viability component.

The results of the experiments on each of the major components of fitness in many ways explain the results of PROUT (1971a, b), BUNDGAARD and CHRISTIANSEN (1972) and others where the fitnesses for each component were measured in a population. Any chromosome that has a quasinormal viability and is not sterile or semisterile when homozygous is likely to show more adverse effects in adult males than in either larvae or adult females. This 15 to 50% lower mean fitness in adult males could easily result in virility dominating the dynamics of a selection experiment. It would also indicate that there is a large potential for virility selection in nature; ANDERSON *et al.* (1979) did indeed find virility selection occurring in natural populations of *D. pseudoobscura*.

The consequences of selection among males on the dynamics of a population are as yet unclear. Genetic load as defined by MORTON, CROW and MULLER (1956) and CROW (1958) is a simple function of fitness; the results reported here, or those of ANDERSON *et al.* (1979), can be transformed into terms of genetic load. Yet, the genetic load due to males may not affect the population. As is well known among demographers, the sexes are not equal in their effects on population dynamics. In fact, they ignore males altogether. Any aspects of the larval and adult male components that do not affect or are not correlated with female survival, fecundity or fertility would in effect be neutral to population dynamics, as long as all females are mated. The result of this lack of ecological effects is that a large amount of selection could occur among males, including selection for secondary sexual characters, chromosomal polymorphisms, and so on, with no detriment to the population.

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