

AN EXPERIMENT ON MIGRATION AND SIMULTANEOUS SELECTION FOR SEVERAL TRAITS IN *DROSOPHILA PSEUDOOBSCURA*¹

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ANIMAL and plant breeders often face the problem of selection for several characters simultaneously, but laboratory experiments on selection deal usually with a single trait at a time. Even so, comparison of the original strain with that resulting from selection sometimes discloses differences in traits additional to that for which the selection was made. There are several causes which can bring about such correlated responses to selection. One of them is pleiotropism—the genes affecting the trait for which one selects may have manifold effects. Another is linkage—the gene selected may be associated in the chromosomes of a given strain with genes for quite other characteristics. Still another is that an artificial selection for a certain trait may cause a lowering of the fitness, which may then be compensated by natural selection for alleles at other loci. In natural populations, natural selection is likely to occur for several or many qualities at a time, the combination of which results in a satisfactory adaptedness to changing environmental conditions. This was most likely the case in human populations, during the transitions from their pristine state to culture, to civilization, to technologically developed societies. An experimental essay, the results of which are reported in the present article, was contrived as a model of such multiple selection in the fly, *Drosophila pseudoobscura*.

The geotaxis classification mazes, modeled after HIRSCH (1962) and HIRSCH and ERLÉNMEYER-KIMLING (1962), permit screening without undue amount of labor of fairly large numbers of flies in each generation (300 females and 300 males, i.e., a total of 600). The individuals which have made mostly downward, or mostly upward choices in the maze are selected as parents of the succeeding generations. Such selection produces genetically positively or negatively geotactic flies, as shown in *Drosophila melanogaster* by the authors referred to above, and by DOBZHANSKY and SPASSKY (1962, 1967) in *D. pseudoobscura*.

WADDINGTON (1959, 1960) selected *D. melanogaster* for the ability of the larvae to survive feeding on a medium containing as much as 7% sodium chloride. Although *D. pseudoobscura* proved to be less pliant genetically in this respect, we did increase the salt tolerance significantly in the experiments to be reported.

It is well known that the variations in the gene arrangement in the third chromosomes of *D. pseudoobscura* are maintained in natural as well as in experimental

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populations by a heterotic balancing natural selection. The populations used in our experiments were made polymorphic for two gene arrangements, namely Arrowhead (AR) and Chiricahua (CH).

MATERIALS AND METHODS

All experimental populations were maintained in a constant temperature room at 25°C, with only artificial light. The progenitors of the flies used were collected at Piñon Flats, Mount San Jacinto, California in 1948; the strains were maintained in the laboratory, and in 1960–1962 were used in the selection experiments which produced geopositive and geonegative strain; after 18 generations the selection was relaxed, and the strains were maintained since with no further selection for the geotactic behavior (DOBZHANSKY and SPASSKY 1962). The present experiments were initiated in June 1963 and completed in August 1966.

RESULTS

The experimental populations: The foundation stock for the experimental populations was obtained by crossing an AR strain which was preselected for positive geotaxis, and a CH strain preselected for negative geotaxis. In both strains the selection was relaxed for more than a year (see above). The geotactic scores of these strains at the beginning of the present experiments were as follows:

	Arrowhead	Chiricahua
Females	13.14 ± .19	9.05 ± .23
Males	11.68 ± .23	8.28 ± .22

The meaning of these figures is as follows. The geotaxis maze has 16 terminal tubes, of which No. 1, the uppermost, is reached by the flies making 15 upward choices, and No. 16, the lowermost, is reached by 15 downward choices. The middle tubes, Nos. 8 and 9, receive the flies making nearly as many, seven or eight, upward and downwards choices. The geotactic score is computed very simply as the mean of the approximately 300 flies which have passed through the maze and assorted themselves in the terminal tubes. The highest possible negative score, unity, would mean that all the flies went upwards and assembled in No. 1; the highest possible positive, 16, that all the flies reached No. 16; if the flies are neutral to gravity and go upwards and downwards at random, the mean score will be 8.5. It can be seen that the AR strain was still decidedly positive, while CH had relapsed to the neutrality point from its former negative status.

The foundation stocks for the experimental populations were made by crossing the AR and CH flies in the following proportions:

A-populations: 20 pairs (20 females + 20 males) from the CH strain and five pairs (5 females + 5 males) from the AR strain. The initial frequencies of AR and CH chromosomes in the resulting populations were, accordingly, 80% CH and 20% AR.

P-populations: 245 pairs of AR and five pairs of CH. The initial frequencies were, then, 98% AR and 2% CH.

The flies were placed in two population cages, A and P. In the A-cage the nutrient medium was the usual water + molasses + cream-of-wheat + tegosept

mixture used in our laboratory. In the P-cage it was the corn meal + molasses + agar, to which .85% by weight of common table salt was added. In the next generation, 300 virgin females and 300 males were taken from each cage and made to run through the geotaxis maze. The geotactic scores in these parental generation flies turned out as follows:

	A-population	P-population
Females	9.63 ± .24	12.82 ± .19
Males	8.09 ± .22	13.74 ± .22

From these populations the founders were selected for the four experimental populations in the following manner:

A-7, 20 pairs of most geonegative females and males from the A-population, to which were added five most geonegative pairs from the P-population. Ordinary food medium, no salt added.

P-8, 245 pairs of most geopositive females and males from P, and five most geopositive pairs from A. Food medium with .85% salt added.

A-9, 20 most geopositive pairs from A, and five most geopositive pairs from P. Ordinary food medium.

P-10, 245 most geonegative pairs from P, and five most geonegative ones from A. Food medium with .85% salt added.

In all the following generations, up to the end of the experiments, 300 virgin females and 300 males from each population were made to run, of course, separately, through the geotaxis maze. The selection practiced is shown in Figure 1. The A-7 and A-9 populations always had the ordinary food medium, while in P-8 and P-10 salt was added. The original concentration of .85% was raised to 1% in the 8th generation, to 1.2 in the 10th, 1.3 in the 12th, 1.5 in the 13th,

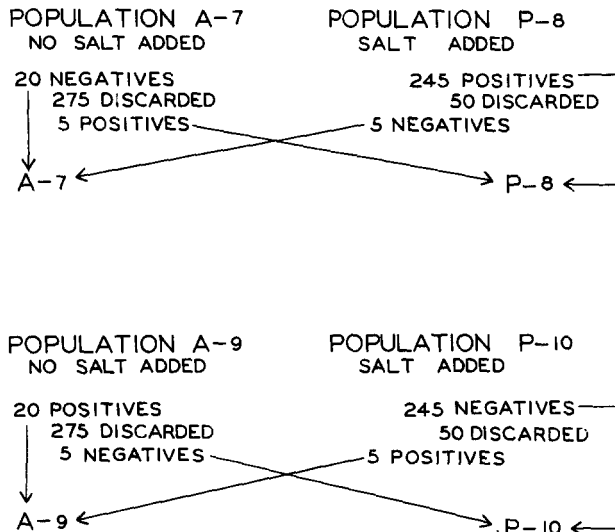


FIGURE 1.—The selection for geotaxis responses in the experimental populations.

1.7 in the 15th, 2.0 in the 18th, 2.2 in the 21st, and 2.5 in the 26th. Populations A-9 and P-10 were discontinued after 14 generations, and A-7 and P-8 after 30 generations of selection.

Our populations A-7 and P-8 exchange migrants in each generation, and so do A-9 and P-10. Exactly five pairs of flies are transferred from population to population; however, since the A-populations are started in each generation with 25 pairs of flies and the P-populations with 250 pairs, the migrants constitute 20% of the parents in A and only 2% in P. Suppose, then, that to start with the genes are all different in A and P populations. After one generation of interchange of migrants, the proportion of the original A genes drops to 80% in the population A, and becomes 2% in the population P. The frequencies converge very rapidly, until the two populations exchanging migrants become alike in having their genes in the same proportions from both original A and P populations. Figure 2 shows the expected proportions of A genes in the population A (the A curve) and in the population P (the B curve). We are obligated to PROFESSORS R. C. LEWONTIN and WYATT ANDERSON for a formula describing the results of the migration. Let XA_n and YA_n be the percentages of "A" genes in the populations A and P respectively after n generations of interchange of migrants, then:

$$XA_n = 90.91 (0.1 + .78^n), \text{ and}$$

$$YA_n = 9.091 (1 - .78^n)$$

The frequencies approach asymptotically the limit of 9.091% A genes in both populations. Of course, the populations are expected to become genetically alike

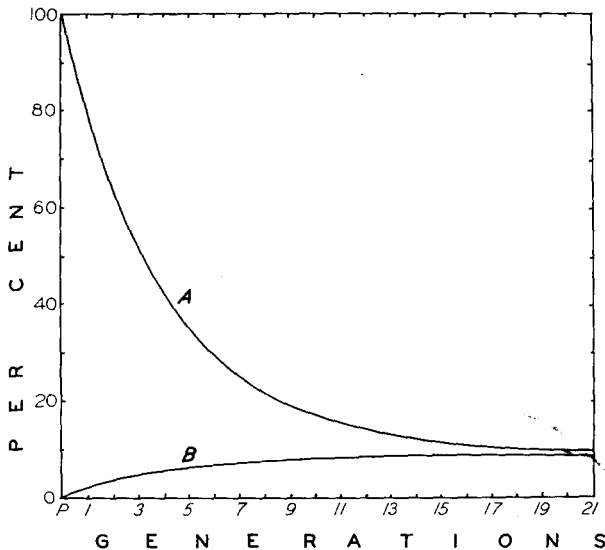


FIGURE 2.—The theoretical rates of genetic convergence due to migration in experimental populations. The curves show the percentages of the genes derived from A-7 and A-9 populations in these populations themselves (the A curve) and in P-8 and P-10 populations (the B curve).

only if the migration is genetically unselective, and the fitness of the migrants and of the receiving populations are alike.

The geotactic behavior: The mean geotactic scores and their variances in the four experimental populations are reported in Tables 1 and 2 and in Figures 3 and 4. Several interesting results can be seen at a glance. Population A-7 was being selected toward negatively, and it did change in the negative direction (Figure 3). However, the same figure shows that population P-8 also became progressively more negative, although it was subject to a weak selection in the positive direction (cf. Figure 1). Moreover, the geotactic scores of these two populations did not converge and become identical, as might have been expected, because of the interchange of migrants. A-7 was at the start geotactically neutral or slightly positive, while P-8 was decidedly positive. After 30 generations of

TABLE 1

The geotactic scores in different generations in the populations A-7 and P-8

Generation	Females					Males						
	Mean	A-7	σ^2	Mean	P-8	σ^2	Mean	A-7	σ^2	Mean	P-8	σ^2
P	9.63	16.32	12.82	10.41	8.09	14.27	13.74	13.85				
1	9.82	17.37	13.33	11.38	9.17	20.34	13.25	10.13				
2	9.92	21.35	14.10	7.27	9.65	18.51	13.04	13.36				
3	9.82	17.54	12.63	9.26	8.19	11.40	11.36	11.90				
4	9.35	18.03	11.89	12.40	8.29	17.32	10.65	14.61				
5	10.62	13.08	11.61	10.95	8.83	17.58	11.03	12.49				
6	9.55	16.91	12.49	9.74	9.28	18.14	11.88	14.61				
7	8.87	13.47	13.06	8.18	8.03	14.56	11.97	11.94				
8	8.49	17.91	13.29	9.43	9.12	20.39	12.39	14.83				
9	9.44	19.74	12.02	13.42	9.54	17.46	11.65	13.71				
10	7.74	19.28	12.99	9.60	8.27	20.49	12.80	9.93				
11	8.47	18.46	12.55	11.13	8.60	16.21	11.24	14.60				
12	7.58	16.72	11.23	17.05	7.83	14.65	10.35	16.58				
13	6.04	12.47	13.20	13.54	7.13	8.34	12.03	14.17				
14	9.71	18.37	12.64	11.62	7.32	13.35	11.43	14.26				
15	8.46	20.64	12.58	10.67	7.33	18.82	11.88	15.08				
16	7.58	19.44	11.27	16.51	8.17	13.83	10.97	14.38				
17	8.88	19.33	12.17	12.71	8.11	15.32	10.94	13.00				
18	8.84	19.83	11.22	14.35	7.68	16.25	11.16	13.44				
19	8.17	21.83	10.88	15.71	7.77	18.80	10.62	13.35				
20	7.81	19.62	10.71	17.61	8.43	16.13	11.76	11.72				
21	8.65	19.55	10.79	11.15	8.24	21.56	11.44	11.66				
22	9.69	15.00	11.06	17.17	9.27	15.24	10.95	14.51				
23	6.73	12.76	11.19	14.26	6.52	13.02	11.37	12.68				
24	9.10	11.18	10.49	9.42	6.64	12.30	9.72	10.71				
25	8.02	13.32	10.04	14.49	6.74	11.53	8.72	14.29				
26	8.28	18.16	11.18	14.96	6.57	13.52	9.31	16.08				
27	8.55	17.02	11.19	14.95	6.44	16.18	9.98	15.17				
28	8.32	19.03	11.68	13.85	7.05	15.07	11.83	12.69				
29	9.35	17.92	11.29	12.33	6.42	15.33	10.39	17.30				
30	8.23	13.57	10.11	10.60	6.93	14.20	9.13	11.09				

TABLE 2

The geotactic scores in different generations in the populations A-9 and P-10

Generation	Females					Males						
	Mean	A-9	σ^2	Mean	P-10	σ^2	Mean	A-9	σ^2	Mean	P-10	σ^2
P	9.63	16.32		12.82	10.41		8.09	14.27		13.74	13.85	
1	11.69	16.34		13.39	9.59		8.86	18.66		13.76	9.14	
2	10.74	17.76		13.98	7.66		9.67	15.86		13.20	11.65	
3	11.69	10.59		12.99	9.99		10.69	11.65		11.87	11.31	
4	11.22	13.97		11.59	19.35		11.44	13.01		10.14	18.05	
5	12.70	8.71		13.13	9.39		12.19	13.15		10.10	17.91	
6	13.18	9.19		11.48	12.47		12.24	9.51		12.26	10.53	
7	13.22	7.60		10.21	11.77		12.00	13.93		8.89	16.07	
8	12.67	11.88		12.63	11.40		12.81	11.75		12.09	15.02	
9	13.03	10.03		11.02	14.35		12.55	10.42		11.79	11.27	
10	13.01	8.90		10.95	13.01		13.21	8.72		11.32	13.60	
11	11.68	11.11		12.87	10.89		11.69	10.89		12.37	11.47	
12	13.42	10.78		12.13	13.68		12.90	11.43		11.62	13.00	
13	13.97	11.02		10.58	11.92		13.51	10.43		10.97	15.41	
14	13.83	9.87		10.27	11.70		13.27	11.54		10.52	17.22	

selection, the males in A-7 became geotactically negative while the females became neutral or slightly negative. P-8 changed toward neutrality, but still remained clearly positive.

The situation is strikingly different with A-9 and P-10 (Figure 4). A-9 was originally like A-7, but A-9 was selected in the positive direction (Figure 1). It did change toward a greater positivity, and although the experiment was interrupted after 14 generations of selection, the A-9 flies exhibited a very pro-

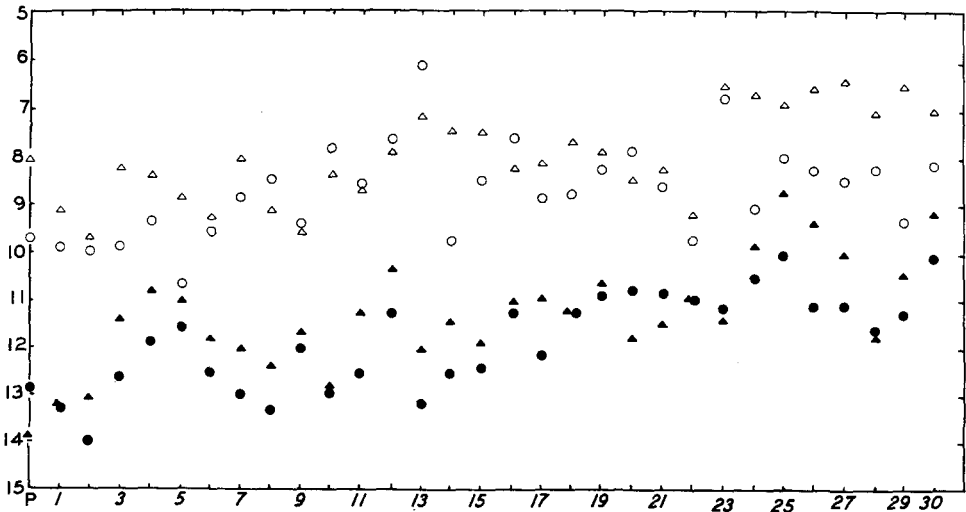


FIGURE 3.—The mean geotactic scores (ordinate) in different selected generations (abscissa) in populations A-7 (white symbols) and P-8 (black symbols). Females—circles, males—triangles.

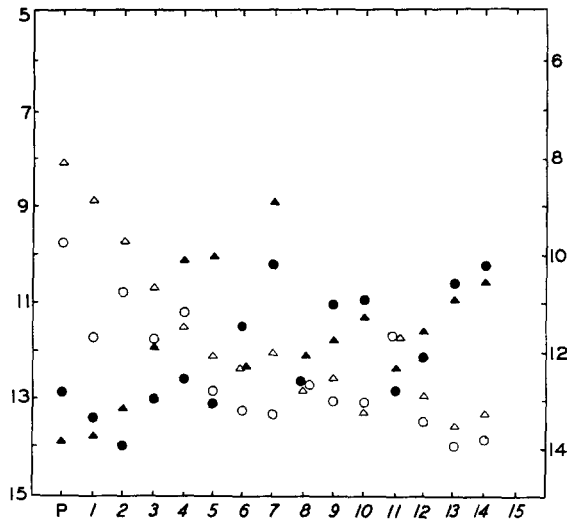


FIGURE 4.—The mean geotactic scores in populations A-9 (white symbols) and P-10 (black symbols). Females—circles, males—triangles.

nounced positive geotactic behavior. Now, P-10 was more positive to start with than A-9 and it was subject to only a weak negative selection (50 most positive flies out of 300 discarded, and five most negative pairs from A-9 added). Nevertheless, it changed in the negative direction, more precisely toward neutrality. By about the 5th and 6th generations of the selection, A-9 and P-10 had similar geotactic scores. But instead of remaining at this common average, P-10 continued to move in the negative direction, not quite reaching neutrality when the experiment was discontinued.

Resistance to salt in the food medium: As indicated above, the amount of sodium chloride added to the medium on which the populations P-8 and P-10 developed could only be increased very gradually, if the population cage treated was to produce at least the 300 females and 300 males needed for the selection for the geotactic behavior. Comparison of our data with those of WADDINGTON (1959, 1960) suggests that *D. pseudoobscura* is more sensitive to salt than *D. melanogaster*, although the different techniques in the experiments make this not quite certain.

Since we were able to maintain the populations P-8 and P-10 on food with increasing amounts of salt, it follows that a resistance to salt did develop in these populations. The question that suggests itself is whether the populations A-7 and A-9 became also salt resistant. These latter populations were maintained on food with no salt added, but on the other hand they were continually receiving migrants from the P-populations. Tests were arranged as follows. Three kinds of population cages were set up, with nutrient media to which 3% salt, 2.5%, or no salt was added. Each cage had 15 cups with nutrient medium. Into each cage were introduced about 250 pairs of flies of one of the following three kinds: (A) from the population P-8 after 30 generations of selection, (B) from A-7

after it had received immigrant from P-8 for the same number of generations, and (C) control flies, which were an F_2 generation from the cross of AR and CH strains which were also the original parents in the A and P populations. The flies were left to oviposit for 4 days, whereupon the adults were discarded, the cups with the eggs and larvae in them withdrawn, plastic "chimneys" attached to each cup, provided with cotton plugs, and allowed to develop at 25°C. The adult flies hatching in the cups were then counted. The results are summarized in Table 3. Mean numbers hatching per cup, as well as the maximal and minimal numbers of the flies among the 15 cups in a given cage, are shown.

The results could hardly be clearer. Although control flies oviposit on the medium with a 3% salt added, none develop to the adult stage. Very few survive on this salt concentration in the progenies of A-7, and considerably more in the progenies of P-8. The same sequence of survival rates is observed on the media with 2.5% salt. The survival is however below that on the media with no salt added, even in the case of the most adapted population, P-8.

WADDINGTON found a pronounced increase of the anal papillae in the larvae and pupae from the populations of *D. melanogaster* which became adapted to survive on food with high salt concentrations. This change proved not to be noticeable in the pupae of P-8 formed in the cups with 3% salt concentration. This may be a morphological expression of the greater adaptability of *D. melanogaster*, compared to *D. pseudoobscura* to saline media.

Gene arrangements in the third chromosomes: As stated above, the initial frequencies of AR and CH third chromosomes in the A-populations were 20 and 80% respectively, and in the P-populations 98 and 2% respectively. Even if the A and P populations were not exchanging migrants, the chromosome frequencies would be expected to change. In experimental populations containing these two kinds of chromosomes, kept at 25°C on ordinary food medium and not selected for geotaxis, natural selection establishes an equilibrium at values of between 70 and 80% AR and 20 to 30% CH. DOBZHANSKY and SPASSKY (1962) found, however, in their older experiments that selection for negative geotaxis favored AR chromosomes, and selection for positive geotaxis favored the AR/CH heterokaryotypes. In the newer experiments (DOBZHANSKY and SPASSKY 1967), carried

TABLE 3

Mean, maximal and minimal numbers of flies hatching per food cup in three different populations and on three different media

Population	Salt added to the culture medium		
	None	2.5%	3%
Control	190.86 (80-344)	1.40 (0-6)	0 (0)
A-7	171.07 (44-304)	43.66 (15-74)	0.47 (0-2)
P-8	242.20 (195-315)	85.06 (20-170)	4.87 (0-21)

out under conditions only slightly different from the old ones, the signs of the correlated effects were almost reversed, the negative selection now favoring CH chromosomes, while positive selection giving equilibrium values for AR and CH almost similar to those obtained without a selection for geotaxis, or slightly more in favor of AR. Such "unpredictability" may be not uncharacteristic of correlated effects of selections—they depend on what genes happen to be associated in the chromosomes with the genes determining the traits under artificial selection.

Table 4 reports the frequencies of AR chromosomes in the populations A-7 to P-10. The figures for June, 1963, are the frequencies among the founders, while all other figures are based on cytological examination of samples of 300 chromosomes per population at each date. The frequencies of AR rose in A-populations and decreased in P-populations. However, even after 3 years of selection, AR remained less frequent in A-7 (selected for negative geotaxis) than in P-8 (where there was a weak selection for positive geotaxis). In populations not selected for geotaxis, AR-CH equilibrium values are approached within a year from the start, and the interchange of migrants could only speed up the process. The situation of A-9 and P-10 is even more interesting. Although AR was at the start less frequent in A-9 than in P-10, about 15 months later A-9 had slightly more AR than did P-10. Moreover, while the final frequencies in A-7 and A-9 were approximately equal, AR fell in P-10 much more than it did in P-8. All this is consistent with selection for positive geotaxis favoring AR more than CH, while selection for negative geotaxis doing the reverse.

DISCUSSION

It is evident that certain genetic changes in three different traits have taken place in our experimental populations. The traits are geotactic behavior, salt resistance, and chromosomal variation. Both A and P populations have changed. We must now inquire whether these changes were the same or different from those observed in experimental populations in which the selection is directed at a single trait only. Relevant data are available in *D. pseudoobscura* for two of the three traits: geotactic response and chromosomal polymorphism.

DOBZHANSKY and SPASSKY (1967) have computed the realized heritability for the geotactic behavior over 15 generations of selection in populations submitted to a directional selection, and in populations receiving migrants from other popu-

TABLE 4

Percentage frequencies of AR third chromosomes in the experimental populations

	A-7	P-8	A-9	P-10
June 1963	20.0	98.0	20.0	98.0
November 1963	26.3	71.3	28.3	69.3
August 1964	63.0	55.7
January 1965	51.7	81.3
September 1966	66.3	83.0

lations which were themselves selected for a different trait (phototaxis). The calculations (following FALCONER 1955, 1960) are made as follows. For each generation we know the mean geotactic score of the population, as well as the mean score of the individuals (the 245 or the 20 pairs) selected. The difference is the selection differential. We also know the mean score of the population from which the migrants came, and the mean score of these migrants (five pairs). The mean scores in the populations in successive generations indicate the selection response. The regression slopes of the mean scores plotted against the cumulated selection differentials give estimates of the realized heritability. Under directional selection DOBZHANSKY and SPASSKY obtained the following estimates:

	<i>Positive selection</i>	<i>Negative selection</i>
Females	+ .0316 ± .0045	+ .0244 ± .0111
Males	+ .0206 ± .0068	+ .0336 ± .0089

In pairs of populations exchanging migrants the estimates were:

	<i>Positive selection</i>	<i>Negative selection</i>
Females	+ .0099 ± .0100	+ .0547 ± .0121
Males	+ .0287 ± .0101	+ .0156 ± .0089

The calculations for A-7 and A-9 populations yielded these estimates:

	<i>A-9 (Positive)</i>	<i>A-7 (Negative)</i>
Females	+ .0804 ± .0158	+ .0243 ± .0084
Males	+ .1053 ± .0128	+ .0143 ± .0108

The realized heritability of the geotactic response is low. The fact which concerns us most here is, however, that the estimates for A-9 are significantly above those obtained for A-7. This is in spite of the fact that the foundation stocks of both populations were the same. Still more interesting is the performance of P-8 and P-10 populations. The geotactic score of P-8 shifted in the negative direction, or more precisely toward neutrality, in spite of the selection having been in the positive direction. In P-10 the change was sharply negative. The realized heritability estimates for P-8 are negative, for P-10 positive and very high. Now, negative heritability is biologically nonsense; negative estimates came about because, although the selection differentials in P-8 were positive, the selection response was negative.

It is evident that in addition to the artificial selection for geotactic behavior applied in our four experimental populations, they were subject to other selective pressures which, at least in P-populations, were stronger than the artificial selection. Such pressures could come from two sources. First, the P-populations were exposed to selection by salt-containing media. We do not know whether a shift toward geotactic neutrality or negativity is a correlated response to the selection for salt resistance. Secondly, we may be dealing with LERNER's (1958) genetic

homeostasis. Unselected strains of *D. pseudoobscura* are usually geotactically neutral on the average (DOBZHANSKY and SPASSKY, unpublished data). Upon relaxation of artificial selection, the selected geopositive and geonegative strains tend to relapse toward neutrality (DOBZHANSKY and SPASSKY 1962). A glance at Figures 3 and 4 shows that both P-8 and P-10 started at a level clearly deviating from neutrality in the positive direction, while A-7 and A-9 were to begin with neutral.

On such a basis the experimental results make sense. In P-8 the weak artificial selection toward positivity was unable to compensate for the homeostatic trend toward neutrality; in P-10 the artificial selection and the homeostatic trend were mutually reinforcing, and the population changed rapidly. At the same time, population A-7, selected for negativity, was receiving immigrants from a more positive population; the trend of change was weakly negative. Population A-9 was selected toward positivity and received positive immigrants; it changed toward positivity so rapidly that it became more positive than P-10. As a consequence, A-7 and P-8 did not converge in their geotactic scores, despite the gene exchange. A-8 and P-10, on the contrary, converged very rapidly, but then diverged again in opposite directions.

The chromosomal polymorphism showed an equally interesting behavior. AR chromosomes were at the beginning rare in A but frequent in P-populations. A-7 and P-8 failed to reach a common equilibrium after 30 generations (more than 3 years), although such equilibria are reached generally within about one year. A-9 and P-10 not only converged, but AR became more frequent in A-9 than in P-10. This is a response correlated with the selection for geotactic behavior, rather than with that for salt tolerance. This seems clear enough, since P-8 and P-10 were both raised on salty food but the frequencies of AR and CH chromosomes evolved in them quite differently. Starting from a common source, the diversifying (disruptive) selection has produced four populations genetically distinct in three different traits.

We wish to thank PROFESSOR WYATT ANDERSON for statistical advice throughout the work, PROFESSOR R. C. LEWONTIN for the formula describing the genetic results of the exchange of migrants between the populations, and MRS. OLGA PAVLOVSKY for making the slides in which the salivary gland chromosomes were examined.

SUMMARY

Diversifying selection has been applied to two pairs of populations, A-7 and P-8, and A-9 and P-10. A strong selection for negative or for positive geotaxis was made in A-populations, only weak selection in P-populations, and a strong selection for migrants which these populations were exchanging at a fixed rate in every generation. Moreover, A-populations developed on ordinary culture media, while progressively greater concentrations of NaCl were added to the media in P-populations. All the populations descended from a common source, and were polymorphic for AR and CH gene arrangements in the third chromosomes.—Despite the continuous gene exchange, the artificial and natural selec-

tions resulted in four genetically distinct populations. Changes were observed in the geotactic behavior, salt tolerance, and chromosomal composition. Correlated responses to selection were pronounced; in one population a correlated response resulted in an appearance of "negative" heritability, in another a simulation of a high heritability. The salt tolerance selected in P-populations was partly transferred by the migrants to A-populations.

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