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Author(s): Th. Dobzhansky and B. Spassky  
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# Effects of selection and migration on geotactic and phototactic behaviour of *Drosophila*. I.

BY TH. DOBZHANSKY, FOR.MEM.R.S., AND B. SPASSKY

*The Rockefeller University, New York City*

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[Plate 7]

Starting with a population of *Drosophila pseudoobscura* which was neutral to light and to gravity, we have obtained by directional selection photopositive and photonegative, as well as geopositive and geonegative descendants. The heritability of the phototactic and geotactic responses is, under the conditions of the experiments, rather low. The realized heritability over the first fifteen generations of selection is between 8 and 10 % for phototaxis, and about 3 % for geotaxis. Despite so low a heritability, these behavioural traits can be sharply modified by selection.

Pairs of populations were made to exchange 20 % of their members in each generation. One population of each pair was selected for phototaxis and the other for geotaxis. The experimental model of the process which is known as 'social mobility' in human populations was so contrived that the migrants taken from the donor populations were phenotypically contrasting with the individuals selected to perpetuate the donor populations themselves. The donor populations changed, as expected, in the directions in which they were being selected. The genetic changes caused in the recipient populations by the immigrants were more interesting. They went in the same directions in which the populations from which the immigrants came were changing. With characters of low heritability, phenotypic rejects coming from genetically improving populations may transmit the genetic improvements to the recipient populations.

## INTRODUCTION

The strategy usually followed in experimental science is to subdivide the phenomena observed into simplest components amenable to study. These components are then removed from, or introduced into, the experimental systems, preferably one by one. Geneticists like to work with single genes producing discrete, easily detectable effects. Many heritable trait differences are, however, polygenic. Perhaps the greatest achievement to date in the study of polygenes is the isolation of the components of a polygenic system by Thoday and his colleagues (Thoday 1961; Wolstenholme & Thoday 1963).

With many biological phenomena, the reductionist, Cartesian, method must, however, be superseded by the compositionist, Darwinian, approach (Simpson 1964; Dobzhansky 1964). These phenomena are complex patterns of relatively simple components; the attention of the investigator is directed towards the patterning rather than towards the components. The genetic processes which take place in human populations, particularly those which concern socially significant traits such as intelligence and special abilities, are highly complex. For obvious reasons, they can be investigated experimentally only by means of models, for the construction of which suitable animals are utilized. Even with animal populations, the investigator must deal with situations more complex than those met in ordinary genetic experiments.

[ 27 ]

In a brilliant theoretical paper, Halsey (1958) discussed the relationships between social mobility and gene exchange in a class society. He assumed a 'low' class nine times more numerous than a 'high' class, and a social mobility such as to replace 10 % of the high class not carrying a 'gene for intelligence' with an equal number of migrants from the low class who do carry this gene, and vice versa. It takes only seven generations to produce a high class in which everybody is a carrier of the gene in question; however, the incidence of this gene in the low class is scarcely diminished in the process.

Halsey's model may well be used as a basis for experimental study of the genetic processes which may be taking place in human societies. The number of its variants is only limited by one's imagination, and by the labour involved. To be even remotely realistic, the models should envisage polygenic rather than monogenic traits as determinants of the 'social mobility'. The animal chosen as experimental material should have a reasonably short generation time, and the traits should be easily measurable. These desiderata are satisfied by the geotactic and phototactic reactions of *Drosophila*. Hirsch and his students constructed a classification maze to measure the geotactic response, and showed that *D. melanogaster* can be selected to give clearly geopositive and geonegative lines (Hirsch 1962; Hirsch & Erlenmeyer-Kimling 1962; Erlenmeyer-Kimling, Hirsch & Weiss 1962). Dobzhansky & Spassky (1962), using a maze constructed under Professor Hirsch's direction, showed the same to be true of *D. pseudoobscura*. Hadler (1964*a, b*) modified Hirsch's maze to serve for measurement of phototaxis, and showed that positively and negatively phototactic *D. melanogaster* can be selected.

In 1962, we initiated experiments on selection of *D. pseudoobscura* for positive and for negative reactions to light and to gravity. The experimental populations are mostly in pairs, some migration ('social mobility') between the two populations taking place in each generation. Several different models have been made; the two populations of a pair may be of unequal size, one starting in each generation with 10 times as many flies as the other, but both being selected for the same trait, geotaxis; or else, the populations are of equal size, but are selected for different traits, one for geotaxis and the other for phototaxis. In the present communication we describe the relatively simple situation, the equal-sized populations, as well as the experiments on directional selection without migration, which serve as controls.

#### APPARATUS AND MATERIAL

The classification mazes for geotaxis and phototaxis are shown in figures 1 and 2, plate 7, respectively. They were built at the instrument shop of the Rockefeller University, following with some variations the models of Professor Hirsch and Mr Hadler. Females or males, numbering 300, are introduced into the starting tube (on the right in figure 1, with a sheet of paper inserted for clarity, on the left in figure 2). The flies pass through plastic cone-shaped funnels, and make fifteen choices of upward or downward directions on the geotaxis maze, or of light or dark passages on the phototaxis maze. The flies emerge finally into terminal tubes, numbered from 1 (uppermost) to 16 (lowermost) on the geotaxis, and from no. 1



FIGURE 1. A classification maze for selection of *Drosophila* for geotactic behaviour. The flies are introduced in the tube on the right, and assort themselves into the sixteen tubes on the left.

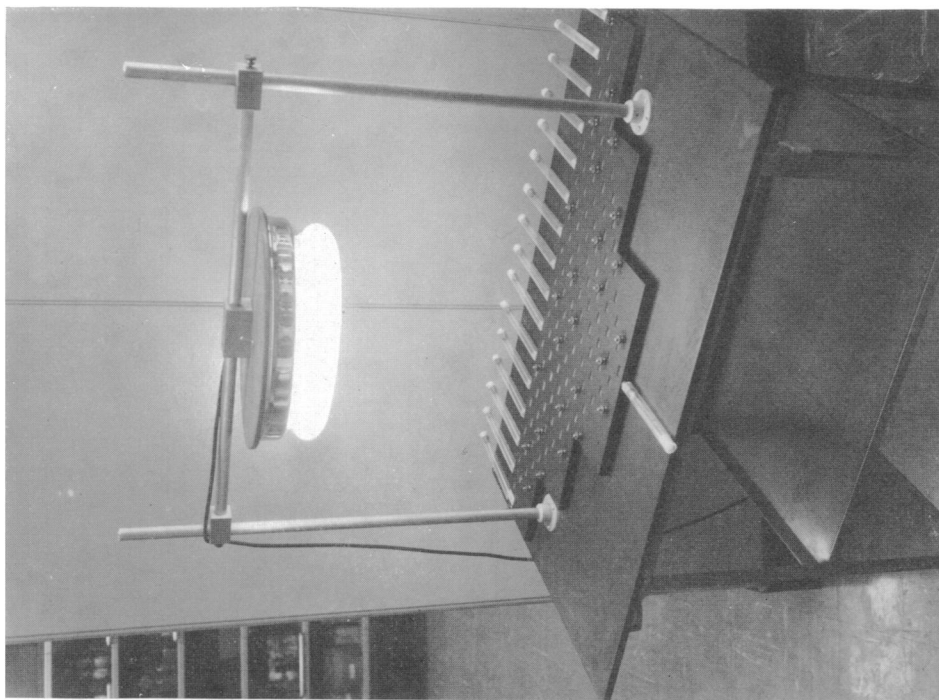


FIGURE 2. A classification maze for selection of *Drosophila* for phototactic behaviour.

(Facing p. 28)

(all dark) to no. 16 (all light passages) on the phototaxis maze. Individuals which make equal numbers of upwards and downwards, or light and dark choices, enter the tubes nos. 8 and 9. It takes approximately 24 h (at 25 °C) for almost all the flies to run through the mazes; the terminal tubes contain small amounts of a nutrient medium. Counting the numbers of the flies in the different tubes, one can compute the means and variances of the geotactic scores, or the phototactic scores, which reflect the numbers of the upwards or downwards, or light or dark passages which the flies have made. A score of 8.5 means a geotactic or phototactic neutrality; the highest positive score is 16, the highest negative is 1.

The flies selected for breeding are 25 females and 25 males, with the highest or the lowest scores, as desired, i.e. flies which have entered the terminal tubes with the highest or with the lowest numbers on the geotaxis or the phototaxis mazes. The females and the males are run through the mazes separately, to keep them virgin. The flies selected (a total of 50) are placed in a plastic population cage with 15 food cups (a variant of Dr M. Strickberger's model). The population cages are kept in a constant temperature room at 25° C, with only artificial light. When pupae are formed in the cups, the cups are withdrawn from the cages, plastic 'chimneys' are attached to each, the flies that hatch are collected daily, females and males stored separately until approximately 300 of each sex are available to be run through one of the mazes. Flies less than 2 days old are not used in the mazes, nor are flies more than 10 days old used.

*Drosophila pseudoobscura* strains descended from wild progenitors collected at Piñon Flat, California, are the experimental material. Of these strains, 10 are homozygous for the *AR*, and 10 others for the *CH* gene arrangement in the third chromosome (see Dobzhansky 1961). The initial populations with which the selection experiments start are prepared by crossing females from all the *AR* strains to males from all *CH*, and vice versa. The frequencies of *AR* and *CH* chromosomes in the founders of the selected populations are, therefore, equal.

#### DIRECTIONAL SELECTION

The mean phototactic scores and their variances in different generations of selection are shown in table 1, and the progress of the selection is represented graphically in figure 3. The starting population was phototactically neutral—the mean scores of 8.70 and 8.64 for the females and males respectively do not differ significantly from exact neutrality, 8.5. Selection causes divergence of the mean scores in the positive and negative lines. After about twelve generations the divergence is so pronounced that only stray individuals of the selected lines enter the 'neutral' tubes nos. 8 and 9.

The variance generally declines as the selection progresses. This does not necessarily mean that the selected populations become uniform for the genetic factors influencing the phototactic response. The normal bell-shaped distribution of the initial population becomes more and more skewed as the selection progresses, because the flies cannot go higher than the terminal tube no. 1 or lower than no. 16.

TABLE 1. DIRECTIONAL SELECTION FOR PHOTOTACTIC RESPONSE, SHOWING MEAN SCORES AND VARIANCES IN DIFFERENT GENERATIONS

generations	females				males			
	positive 20		negative 18		positive 20		negative 18	
	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$
<i>P</i>	8.70	7.50	8.70	7.50	8.64	9.15	8.64	9.15
1	7.78	7.56	6.77	5.71	10.00	8.83	7.87	12.78
2	9.13	6.36	6.91	6.24	10.88	9.44	8.85	10.80
3	8.63	7.59	5.42	4.02	10.86	10.85	6.83	10.57
4	10.28	7.97	5.52	3.65	10.24	6.87	6.10	9.85
5	10.84	5.80	5.06	5.19	11.79	9.92	5.80	10.42
6	10.45	5.96	5.76	5.67	11.83	6.26	6.78	10.56
7	11.17	10.32	4.97	4.72	12.70	9.89	5.74	8.19
8	10.67	5.76	5.00	4.62	11.82	8.60	4.72	7.35
9	12.33	4.04	5.43	4.98	13.44	3.43	5.28	9.07
10	11.38	5.29	4.41	5.04	13.74	2.86	5.89	12.66
11	13.14	4.57	4.83	4.06	13.84	3.06	4.69	9.14
12	13.23	3.77	3.20	3.65	13.96	3.31	4.54	7.27
13	13.23	4.52	3.72	3.72	14.28	2.97	5.42	11.65
14	12.40	4.38	3.34	7.55	14.14	2.54	4.68	10.33
15	13.43	3.26	2.37	2.20	14.49	2.08	3.13	4.46
16	14.37	2.28	2.76	2.78	14.71	1.92	3.84	6.28
17	14.16	2.47	2.85	2.92	14.03	2.68	3.59	6.93

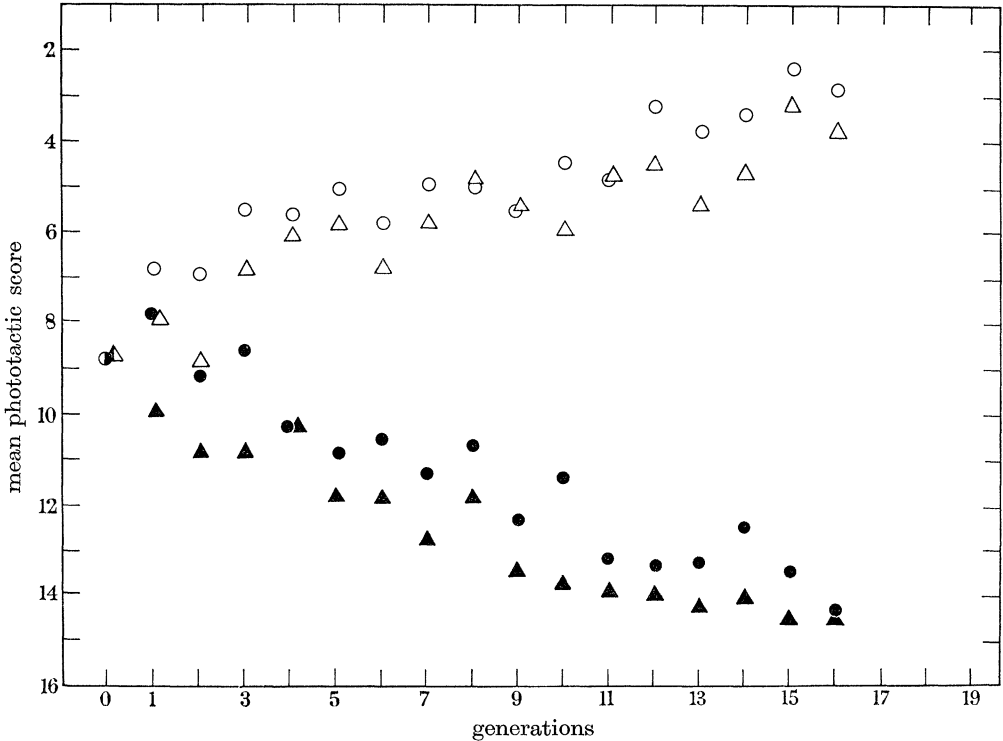


FIGURE 3. Directional selection of phototaxis. White symbols, negative; black symbols, positive selection lines: circles, females; triangles, males.

TABLE 2. DIRECTIONAL SELECTION FOR GEOTACTIC RESPONSE, SHOWING MEAN SCORES AND VARIANCES IN DIFFERENT GENERATIONS

generations	females				males			
	positive 17		negative 19		positive 17		negative 19	
	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$
<i>P</i>	8.24	18.05	8.24	18.05	8.73	15.09	8.73	15.09
1	10.75	12.63	7.89	18.23	10.75	12.54	8.27	13.68
2	10.03	14.65	7.84	15.08	10.99	10.22	7.83	18.62
3	10.36	14.70	7.68	13.98	11.89	9.60	9.42	13.98
4	11.09	13.27	7.10	16.74	11.38	11.87	8.01	14.63
5	10.28	17.27	5.91	12.38	11.72	9.77	6.89	16.19
6	10.33	15.19	6.11	11.00	11.98	10.64	7.64	13.25
7	11.88	11.49	8.42	16.55	11.29	10.14	8.37	12.36
8	11.24	12.40	5.96	10.81	11.35	10.62	6.70	12.58
9	11.98	10.25	5.17	11.46	11.77	10.84	6.07	13.53
10	11.27	14.41	8.15	16.71	11.80	11.32	7.92	15.64
11	12.17	4.49	7.89	16.21	12.62	7.98	5.37	13.45
12	11.64	12.26	5.87	17.46	11.86	10.41	6.27	14.85
13	11.43	12.91	5.92	13.93	11.05	12.19	5.04	10.41
14	12.28	11.66	6.49	15.90	12.84	8.53	7.08	14.52
15	12.14	11.61	4.71	10.02	12.55	10.42	6.08	13.88
16	12.41	14.20	5.38	14.62	12.10	9.73	5.35	12.40
17	12.63	8.85	5.08	16.55	12.75	9.13	4.00	10.10

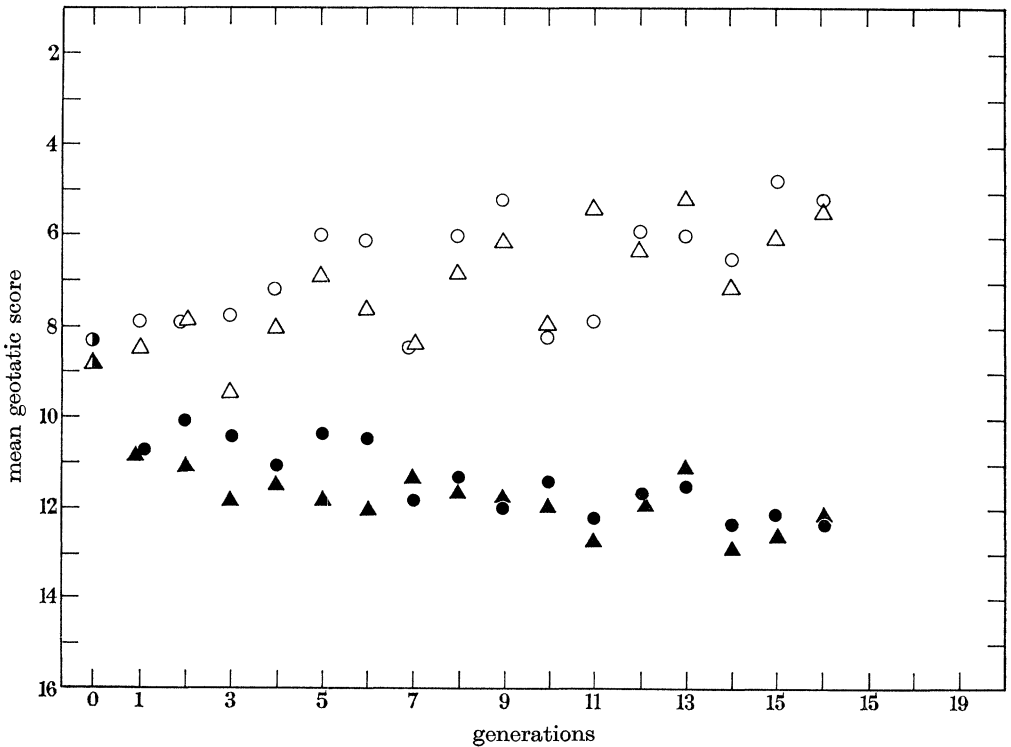


FIGURE 4. Directional selection for geotaxis. Other symbols as in figure 3.

The means and variances of the geotactic scores are reported in table 2 and figure 4. The starting population was geotactically, as well as phototactically, neutral on the average. The selected lines diverge clearly, but not as much as they do in the phototaxis selection. The variances for geotaxis are consistently greater than those for phototaxis, and even after 17 generations of selection the distribution curves of the positively and negatively selected populations overlap broadly on the geotaxis mazes. The variances tend to decrease as the selection progresses, but here again this does not necessarily mean that a genetic uniformity is being approached. The distribution curves of the selected populations are distinctly skewed.

#### HERITABILITY WITH DIRECTIONAL SELECTION

The mean phototactic and geotactic scores of the 300 individuals which were made to run through the mazes in each generation of the selection experiments are shown in tables 1 and 2. The mean scores of the 25 individuals of each sex which were selected in every generation are also known. The differences between the population means and the means of the selected individuals are the selection differentials. The differences between the populations means in the consecutive generations are the selection responses. The ratio of the selection response to the selection differential is obviously a function of the heritability of the trait selected. A ratio of unity means complete heritability, and zero means no heritability (Lerner 1958; Falconer 1960).

The selection differentials between the flies selected in the initial (*P*) generation to give rise to the positive and negative selection lines, the selection responses observed in the first selected generation, and their ratios are as follows:

	differential		response		ratio	
	♀	♂	♀	♂	♀	♂
phototaxis	9.64	10.00	1.01	2.13	0.105	0.213
geotaxis	14.64	14.16	2.86	2.48	0.195	0.175

Between 10 and 21% of the selection differential is passed to the offspring. The heritability is, thus, low. These estimates are not satisfactory because of the sampling errors; for example, the phototactic score in the females of the first selected generation is accidentally too low (see figure 3), and this gives a much lower heritability estimate for the females than for the males. More satisfactory are the estimates of the so-called realized heritability, which are essentially the mean ratios of the selection responses to selection differentials over a series of generations. In figures 5 and 6, the mean scores for each of the 15 generations of selection are plotted against the cumulated selection differentials, as recommended by Falconer (1955, 1960). The regression slopes and their standard errors are then calculated, as follows:

	phototaxis	geotaxis
females, positive selection	0.0996 ± 0.0093	0.0316 ± 0.0045
males, positive selection	0.1005 ± 0.0083	0.0206 ± 0.0068
females, negative selection	0.0912 ± 0.0129	0.0244 ± 0.0111
males, negative selection	0.0762 ± 0.0048	0.0336 ± 0.0089



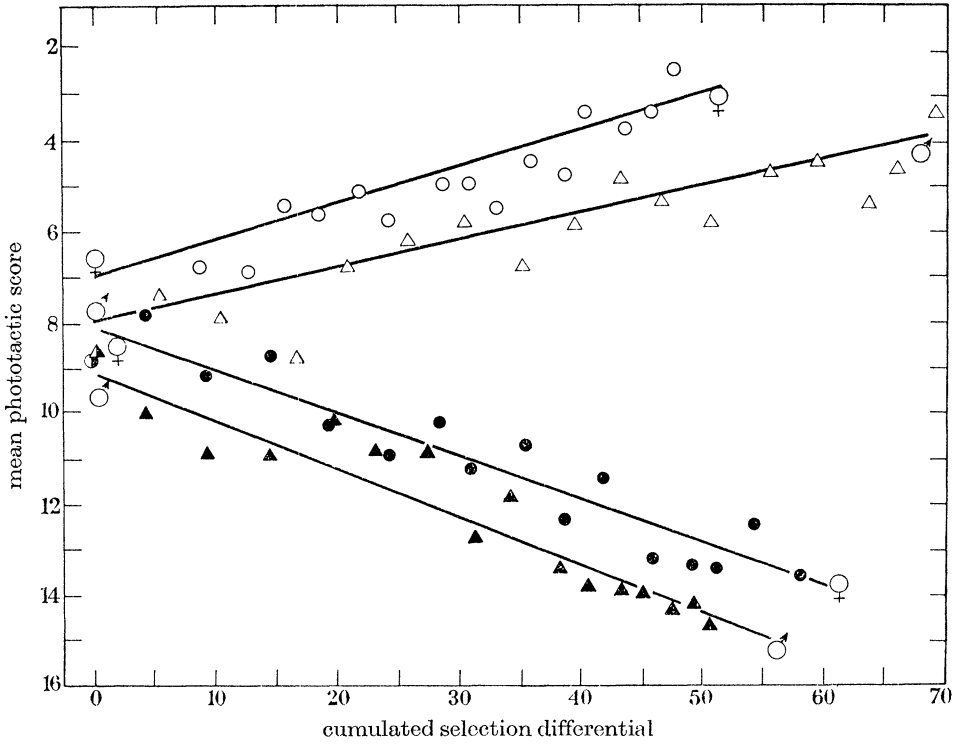


FIGURE 5. Heritability of the phototactic response. Circles, females; triangles, males. The regression lines for positive and for negative selection are shown separately for the two sexes.

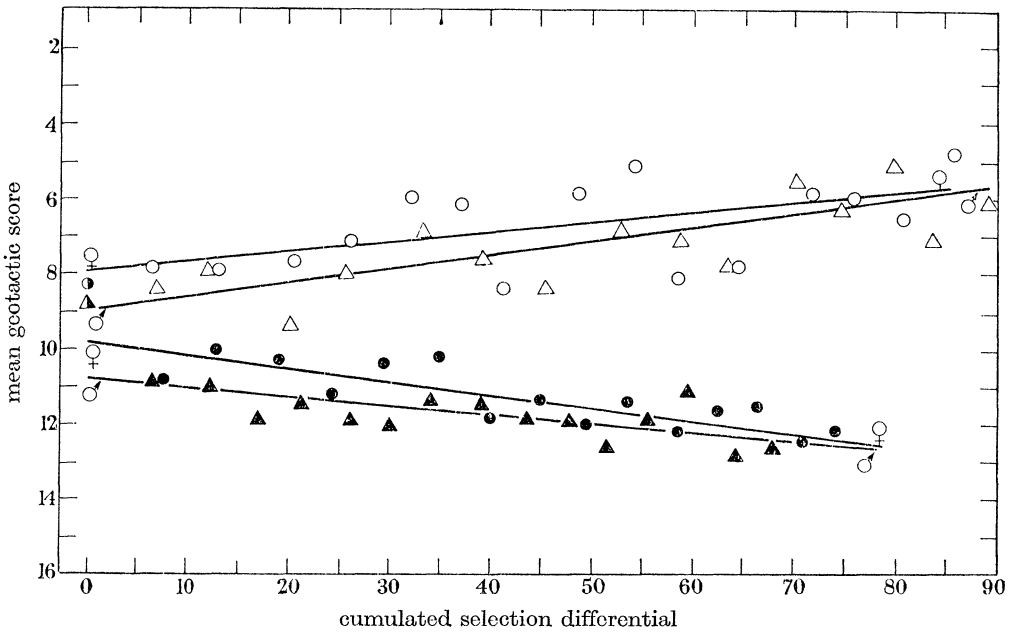


FIGURE 6. Heritability of the geotactic response. Other symbols are as in figure 5.

Averaging the two sexes and the positive and negative selections, the realized heritabilities turn out to be about 9% for phototaxis, and only about 3% for geotaxis. These estimates, especially those for geotaxis, are smaller than those obtained above for the first generation of selection. This is as expected, if the store of the additive genetic variance tends to decrease as the selection proceeds. The regression lines shown in figures 5 and 6 fit the observed data fairly well, but it may be noted that the lines for the positive and the negative slopes for the same sex do not come together at the 0 point of the accumulated selection differential. This indicates again that the heritability tends to diminish as the selection proceeds.

We conclude, then, that the heritabilities of the phototactic and geotactic responses are low. The fact that, despite the low heritabilities, the selected lines diverge as strongly as they do is explained by the selection applied being quite intense—50 individuals out of about 600, or some 8% of the total population being the selected parents of the next generation. Such an intense selection, with avoidance of inbreeding, is possible because of the efficiency of the selecting apparatus—the classification maze devised by Professor Hirsch.

#### POPULATIONS EXCHANGING MIGRANTS

Four experimental populations, nos. 13, 14, 15, and 16 were started as indicated above, i.e. by crossing 10 strains with *AR* and 10 strains with *CH* chromosomes. In every generation, about 300 virgin females and 300 males were obtained from each population. They were run through either the geotaxis or the phototaxis maze, and the following selections (shown schematically in figure 7) were made:

No. 13—passed through the geotaxis maze, to select 20 most positive individuals and five most negative individuals of each sex. The next generation is descended from the 20 geopositive pairs selected in the population no. 13, and five most photopositive pairs transferred from no. 14. The five geonegative pairs selected in no. 13 are transferred to no. 14.

No. 14—passed through the phototaxis maze, 20 most photonegative pairs and five most photopositive pairs are selected. The parents of the next generation are the 20 photonegative pairs, plus five geonegative pairs transferred from the population no. 13. The five photopositive pairs are transferred from no. 14 to no. 13.

No. 15—passed through the geotaxis maze, to select 20 most geonegative and five most geopositive pairs. The parents of the next generation are the 20 geonegatives from no. 15, plus five photonegative pairs from no. 16. The five geopositives from no. 15 are transferred to no. 16.

No. 16—passed through the phototaxis maze, to select 20 most photopositive and five most photonegative pairs. The next generation comes from the 20 photopositives from no. 16 and five geopositive ones transferred from no. 15. The five photonegatives selected in no. 16 are transferred to no. 15.

Migrants were, thus exchanged between the populations nos. 13 and 14, and between nos. 15 and 16. One of the populations of each pair was selected for the geotactic and the other for the phototactic response. The population selected for

geotaxis received migrants from that selected for phototaxis, and vice versa. The migrants were in all cases selected in the opposite direction from the nonmigrants; in other words, each population was sending individuals behaving most differently from the nonmigrants to another population (see figure 7).

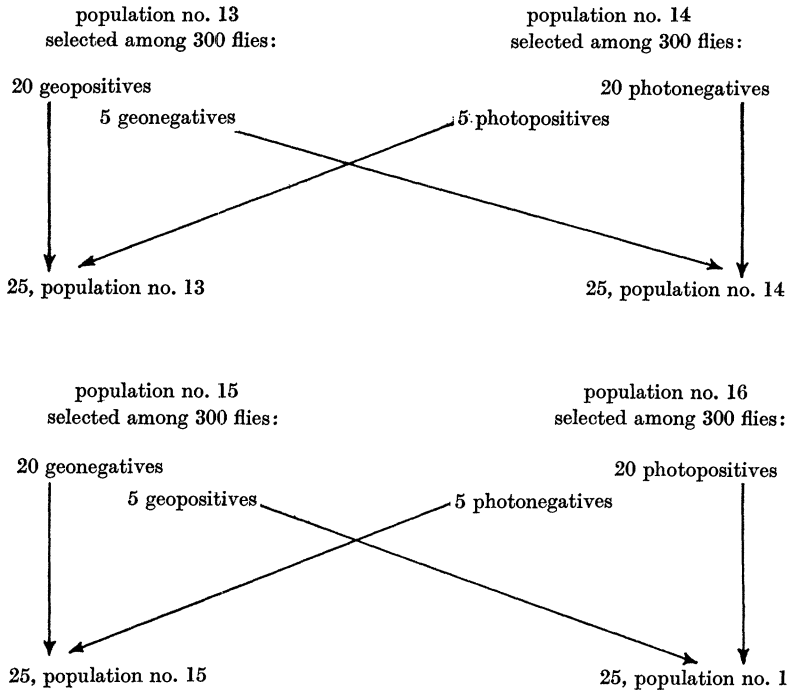


FIGURE 7. The experimental procedure for the study of the interactions between selection and migration.

The geotactic scores in the 25 generations of selection in populations nos. 13 and 15 are shown in table 3 and figure 9, and the phototactic scores in the populations nos. 14 and 16 are in table 4 and figure 8. It is evident that the mean scores of the selected populations diverge; it is also evident that the divergence produced by the selection in the populations exchanging migrants is not as rapid as in those not exchanging them (compare figure 9 with figure 4, and figure 8 with figure 3).

We must now inquire whether the migrants have genetic effects on the populations into which they immigrate. The populations nos. 13 and 15 are selected for geotaxis, but they receive immigrants selected for phototaxis. Conversely, nos. 14 and 16 are selected for phototaxis, but receive immigrants selected for geotaxis. The question is, then, whether the populations diverge both for phototactic and for geotactic responses. In about every fourth generation, the populations were cross-tested, i.e. nos. 14 and 16 were tested for geotaxis and nos. 13 and 15 for phototaxis. The results are summarized in table 5. The means are entered in figures 8 and 9, in which A symbolizes the females and B the males of the population no. 13, C and D the females and the males of no. 14, E and F the females and the males of no. 15 and G and H the females and the males of no. 16.

As expected, the immigrants did cause a genetic divergence of the recipient populations. A closer inspection of the data shows, however, an at first sight quite unexpected effect. Population no. 13 received photopositive, and no. 15 photonegative immigrants. And yet, no. 13 became photonegative and no. 15 photopositive (the letters A stand higher than C, and B higher than D in figure 8).

TABLE 3. GEOTACTIC SCORES IN THE POPULATIONS NOS. 13 AND 15, SELECTED RESPECTIVELY FOR POSITIVE AND FOR NEGATIVE GEOTAXIS, AND RECEIVING IMMIGRANTS FROM THE POPULATIONS SELECTED FOR PHOTOTAXIS

generations	females				males			
	no. 13		no. 15		no. 13		no. 15	
	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$
<i>P</i>	8.76	16.25	8.76	16.25	9.62	14.49	9.62	14.49
1	9.93	14.67	8.98	15.52	10.28	10.13	9.53	12.11
2	9.92	13.63	9.73	18.95	10.02	13.37	8.56	17.58
3	9.87	17.87	9.56	15.13	9.95	14.92	7.16	12.74
4	10.97	12.70	7.91	15.41	8.62	15.81	7.84	13.10
5	11.23	15.05	9.57	16.77	10.86	11.93	9.38	13.31
6	10.63	16.27	7.33	14.27	10.48	13.89	8.08	14.16
7	9.94	16.11	8.22	13.62	11.13	12.18	7.47	14.29
8	10.34	13.42	6.63	13.77	9.64	12.51	7.22	16.77
9	9.71	16.13	5.84	14.68	9.37	12.94	6.57	12.83
10	9.70	14.03	6.25	15.83	10.32	13.57	7.20	15.41
11	11.03	14.85	5.16	14.03	10.90	12.25	7.37	19.20
12	12.27	11.62	6.71	16.05	11.71	10.85	8.06	16.57
13	10.82	14.58	6.74	14.15	11.86	10.29	7.99	14.69
14	10.65	17.51	7.24	17.17	11.19	12.49	7.88	15.49
15	9.86	15.23	6.54	13.68	11.43	10.48	7.55	14.68
16	11.78	12.57	8.72	16.36	10.32	10.06	7.70	12.78
17	11.31	15.37	7.00	15.75	11.51	9.75	9.94	12.57
18	12.35	10.14	5.97	13.94	11.89	11.79	7.00	9.20
19	11.18	15.67	4.60	12.63	11.81	11.07	6.16	14.37
20	12.01	12.80	5.57	14.94	12.41	9.08	7.74	15.38
21	10.20	17.32	7.32	21.48	11.98	11.15	7.05	17.08
22	11.31	15.64	6.26	18.81	11.97	10.02	7.52	16.45
23	10.74	17.91	6.28	16.81	10.64	11.38	7.14	16.20
24	10.62	16.32	6.12	18.25	10.36	12.03	7.49	15.63
25	9.98	16.80	5.17	13.68	10.71	13.05	6.34	15.67

Population no. 14 received geonegative and population no. 16 geopositive immigrants. Yet, figure 9 shows the letter E mostly below G, and F below H, which means that no. 14 became more geopositive than no. 16. This apparent paradox has, as will be shown below, a rather simple explanation: with traits of low heritability, the phenotypic value of an individual may not reflect his genotypic value.

#### HERITABILITY WITH MIGRATION

The experiments with directional selection and without migration have given us estimates of the heritability of phototactic and geotactic responses in the environment and the apparatus used. We may now inquire whether the results

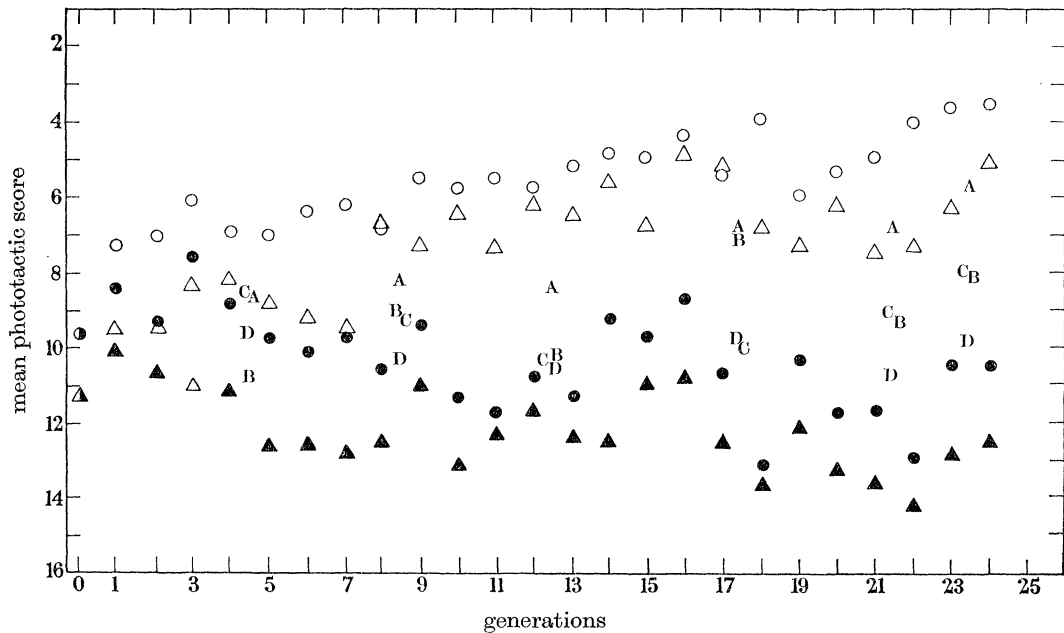


FIGURE 8. The phototactic responses in the population no. 14 (light) and no. 16 (black symbols). Letters A and B give the phototactic scores of the females and males from the population no. 13, and C and D of the females and males from the population no. 15.

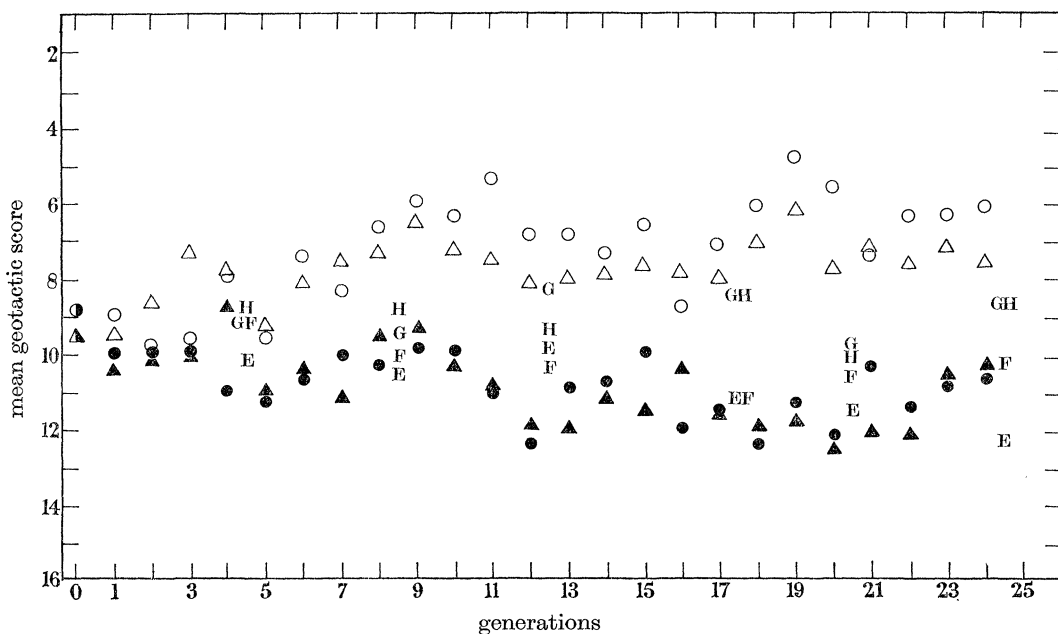


FIGURE 9. The geotactic responses in the populations no. 13 (black) and no. 15 (light symbols). Letters E and F give the geotactic scores of the females and males for the population no. 14, and G and H of the females and males from the population no. 16.

obtained in the populations with migration are compatible with the estimates obtained in the experiments without migration.

The computation of the cumulated selection differentials in the populations nos. 13 to 16 is a rather complex procedure. It will be recalled that these populations descended in each generation from 20 pairs of individuals (80%) selected in the same population, and 5 pairs (20%) of immigrants from another population.

TABLE 4. PHOTOTACTIC SCORES IN THE POPULATIONS NOS. 14 AND 16, SELECTED RESPECTIVELY FOR NEGATIVE AND FOR POSITIVE PHOTOTAXIS, AND RECEIVING IMMIGRANTS FROM THE POPULATIONS SELECTED FOR GEOTAXIS

generation	females				males			
	no. 16		no. 14		no. 16		no. 14	
	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$	mean	$\sigma^2$
<i>P</i>	9.56	6.13	9.56	6.13	11.28	11.21	11.28	11.21
1	8.40	6.27	7.33	6.92	10.09	9.14	9.59	11.41
2	9.36	6.70	7.02	7.21	10.68	6.88	9.36	10.03
3	7.46	6.36	6.12	5.85	11.06	8.38	8.17	12.90
4	8.89	6.94	6.96	7.72	11.12	7.92	8.08	11.53
5	9.75	5.33	7.01	6.16	12.60	6.83	8.79	13.88
6	10.14	6.83	6.37	6.65	12.55	4.84	9.20	12.94
7	9.77	7.23	6.21	5.60	12.72	4.78	9.47	13.20
8	10.69	5.83	6.86	7.03	12.48	6.11	6.73	14.51
9	9.41	8.65	5.48	10.00	11.00	8.56	7.20	7.02
10	11.33	7.49	5.88	5.56	13.14	4.59	6.50	11.92
11	11.71	5.33	5.53	4.40	12.29	6.57	7.29	11.93
12	10.81	8.06	5.71	7.55	11.70	9.87	6.22	9.61
13	11.26	7.40	5.11	5.79	12.33	10.92	6.52	9.45
14	9.19	9.24	4.93	4.40	12.50	10.06	5.62	7.77
15	9.79	11.24	4.96	4.16	10.97	7.31	6.87	10.39
16	8.68	8.17	4.41	4.52	10.92	11.60	4.88	6.11
17	10.79	8.37	5.41	5.88	12.61	6.40	5.11	7.78
18	13.10	6.52	3.94	7.73	13.71	4.21	6.72	9.90
19	10.35	9.49	6.02	6.21	12.15	8.36	7.38	15.09
20	11.83	7.78	5.24	5.22	13.17	4.82	6.21	13.23
21	10.72	11.42	4.96	7.01	13.62	6.67	7.53	11.57
22	12.95	6.11	3.99	5.62	14.26	2.89	7.33	13.16
23	10.42	12.32	3.67	4.37	12.79	8.76	6.34	10.81
24	10.44	10.85	3.50	4.18	12.42	6.58	4.97	10.86
25	11.08	10.64	3.81	6.05	13.23	5.91	5.73	10.75

Knowing the geotactic (or phototactic) scores of the 20 selected pairs and of the parent population, the selection differentials contributed by these nonmigrant individuals is arrived at. These selection differentials are multiplied by 0.8, since the nonmigrants are 80% of the parents of the next generation. The corresponding geo- or phototactic scores of the donor populations are estimated once in four generations (table 5), and the scores of the intervening generations by interpolation. Since the migrants are taken from the donor population without selection for the trait for which the recipient population is selected, their phenotypic value can be taken as equal to the population mean and used to compute the selection differential.

The cumulated selection differentials in populations nos. 13 to 16, and the mean geo- or phototactic scores of these populations, are shown in figures 8 and 9. The regression slopes and their standard errors are calculated on the basis of the first 15 generations only, to make them comparable to those calculated above for the populations without migration. The regressions are represented in figures 8 and 9

TABLE 5. GENETIC EFFECTS OF IMMIGRANTS ON THE RECEIVING POPULATIONS

generation	females				males			
	mean		$\sigma^2$		mean		$\sigma^2$	
	geotactic scores							
	no. 14		no. 16		no. 14		no. 16	
<i>P</i>	8.76	16.25	8.76	16.25	9.62	14.49	9.62	14.49
4	10.18	14.00	9.28	15.01	9.33	13.79	8.68	17.18
8	10.42	14.17	9.57	17.18	10.09	15.72	8.73	16.68
12	9.79	18.45	8.09	15.66	10.27	13.29	9.49	16.51
17	11.11	13.19	8.50	17.87	11.22	8.18	8.48	16.77
20	11.43	13.48	9.73	14.38	10.60	12.26	10.15	14.80
24	12.35	12.87	8.70	15.77	10.26	12.31	8.66	17.27

generation	phototactic scores								
	no. 13		no. 15		no. 13		no. 15		
	<i>P</i>	9.56	6.13	9.56	6.13	11.28	11.21	11.28	11.21
	4	8.63	7.83	8.55	7.59	10.85	9.57	9.48	10.44
8	8.25	7.68	9.24	5.59	9.14	10.32	10.39	13.00	
12	8.49	6.33	10.21	7.49	10.06	9.81	10.32	9.28	
17	6.90	8.74	10.21	14.44	7.01	12.29	9.90	12.25	
20	6.94	6.52	9.35	8.00	9.61	10.87	10.86	12.62	
24	5.77	6.85	7.98	13.74	8.38	10.57	9.74	13.17	

by solid lines for the first 15 generations, and by dashed lines for the subsequent generations. These dashed lines are, of course, extrapolations. The numerical values of the regressions are as follows:

population	phototaxis	population	geotaxis
no. 14, ♀♀	0.0624 ± 0.0085	no. 13, ♀♀	0.0099 ± 0.0100
no. 14, ♂♂	0.0626 ± 0.0110	no. 13, ♂♂	0.0287 ± 0.0101
no. 16, ♀♀	0.0480 ± 0.0172	no. 15, ♀♀	0.0547 ± 0.0121
no. 16, ♂♂	0.0370 ± 0.0195	no. 15, ♂♂	0.0156 ± 0.0089

The values obtained indicate quite low heritabilities, in fact two of the geotaxis and one of the phototaxis values are not significantly different from zero. More important, these values are lower than the estimates derived from the experiments without migration, and in some cases (the heritability of the phototactic response) significantly so.

The discrepancy is explicable. In our computations of the cumulated selection differential we have tacitly assumed that the nonmigrant majority (80 %) and the immigrant minority (20 %) make contributions to the gene pool of the progeny in

proportion to their numbers. This seems in general a reasonable assumption, but we know that it is not warranted in the material we are dealing with. Ehrman, Spassky, Pavlovsky & Dobzhansky (1965) and Ehrman (1966) have shown that the mating success of *Drosophila pseudoobscura* males in populations in which two kinds of males are present, is a function of the relative frequencies of these two kinds.

Excepting mutants and other weak types, when two kinds of males are equally numerous they mate about equally frequently. When one kind outnumbers the other 4:1 (as in the experimental populations with which we are concerned at present), the average mating frequency of the rarer kind of males is very significantly higher than that of the common type. To put it differently, the 20 % of immigrant males contribute more than 20 % of the paternal genes in the gene pool of the next generation. Now, these 20 % are not selected for the trait for which the recipient population is selected; in point of fact, their mean score is usually lower than the mean of the recipient population. Their enhanced breeding efficiency does not assist, and in fact hinders the progress of the selection. The greatly lowered heritability estimates in the populations exchanging migrants do not mean that the photo- and geotactic behaviours have become influenced more by the environment and less by the heredity than they were in the populations without migration.

#### CONTRASTING GENOTYPIC AND PHENOTYPIC VALUES

If two populations, *A* and *B*, exchange 20 % of individuals per generation, and if the migrants and the nonmigrants contribute to the gene pool in proportion to their numbers, then the incidence of *A* and *B* genes in the populations will converge as shown in figure 12. The *A* and *B* populations will be within 7.78 % of gene uniformity after five generations, and within 0.6 % after 10 generations. We are obligated to Dr Wyatt Anderson for the formula for these calculations,  $P_T = (0.6^T + 1) 50$ , where  $P_T$  is the percentage frequency of 'original *A*' genes in the *T*th generation in population *A*, and *T* the number of the generations of gene exchange.  $1 - P_T$  is the frequency of 'original *A*' genes in the population *B* in the *T*th generation. Since minority males breed more effectively than majority males, the equalization may occur even more rapidly (Ehrman 1966).

The genetic changes which the immigrants cause in the recipient populations in our experiments are most interesting. In the populations nos. 13 to 16, the 80 % of the parents in each generation are selected either for geotaxis or for phototaxis. We know that the selection is quite effective, and the populations change in the expected directions. At the same time, these populations receive immigrants, which are selected always in the direction opposite to that in which the donor populations are selected. The migrants entering the recipient populations are, accordingly, phenotypically very different from the individuals selected to perpetuate the donor populations. One might, therefore, expect that the recipient populations will change in the directions opposite to those of the donor populations. The experiments show that this expectation is not realized, and in point of fact the changes that occur are the reverse of the expectation.



Consider the populations nos. 13 and 14. No. 13 was selected for positive geotaxis and its geotactic score rose from about 9 at the beginning to between 10 and 12 in the latter generations (table 3 and figure 9). The emigrants which no. 13 was sending to no. 14 were, however, selected for negative geotaxis. Since no. 14 was selected for a phototactic rather than for geotactic response, the genetic influence of the immigrants should, it would seem, have changed it towards negative geotaxis. Yet, as shown in table 5 and figure 9, it changed instead in the positive direction; the geotactic scores rose from 8.76 for females and 9.62 for males at the beginning to 12.35 and 10.26 for females and males respectively after 24 generations of immigration.

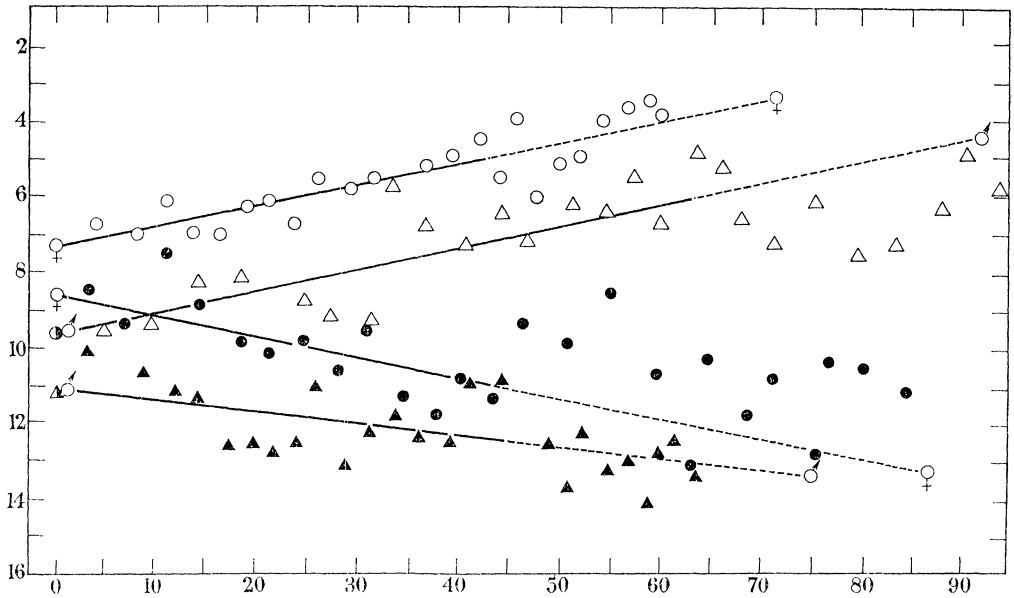


FIGURE 10. The phototactic responses in the populations nos. 14 and 16 plotted in terms of the cumulated selection differentials (abscissa). The regression lines calculated for the first fifteen generations of selection (solid), and extrapolated for later generations (dashed). Other symbols as in figure 8.

The results in the other populations are, at first sight, equally unexpected. Population no. 13 was receiving from no. 14 immigrants selected for photopositivity; yet the phototactic score of no. 13 changed from 9.56 and 11.28 for the females and males at the beginning to 5.77 and 8.38 at the close of the experiments. Populations nos. 15 and 16 were receiving immigrants selected respectively for negative phototaxis and for positive geotaxis. They failed to show consistent changes in either direction, but no. 15 became clearly more photopositive than no. 13, and no. 16 more geonegative than no. 14 (see table 5 and figures 9 and 10).

What is the explanation of this, at first sight so surprising behaviour? We must bear in mind that all donor populations were being selected, during the entire course of the experiments, by taking 20 flies phenotypically contrasting with the five flies which were sent as immigrants to other populations. Since the main selection effects were in the direction of the 20 nonmigrants, the migrants, though

phenotypically contrasting with the nonmigrants, were coming from populations that were undergoing changes in the direction opposite to that in which the migrants were selected. In most populations, the migrants were phenotypically less and less extreme as the selection progressed, and their phenotypes might have reflected less and less accurately their genotypes. The fact nevertheless remains that the flies selected in the donor population and transferred to the recipient one were phenotypically deviating from the mean of the recipient in the direction opposite to that in which the recipient was changing. To put it in another way, the phenotypic 'rejects' from genotypically improving populations may, where characters of low heritability are concerned, convey genetic 'improvements' to the recipient populations.

The matter may be stated in quantitative terms as follows: table 5 gives the data for the geotactic scores for some of the generations in the recipient populations. The scores for the intervening generations are obtained by interpolations. The average phenotypic scores of the migrants transferred can easily be computed from the raw data; the differences between the population averages and the migrants are the selection differentials; these selection differentials are multiplied by 0.2, since the migrants are one-fifth of the parents in the recipient populations. The resulting values are added together, to give the cumulated selection differentials (taking, of course, the positive and negative signs of the selection differentials in consideration). The value for 24 generations of selection and migration are as follows:

	females	males
geotaxis, population no. 14	-44.76	-39.63
geotaxis, population no. 16	+35.23	+34.10
phototaxis, population no. 13	+22.53	+24.78
phototaxis, population no. 15	-30.26	-30.94

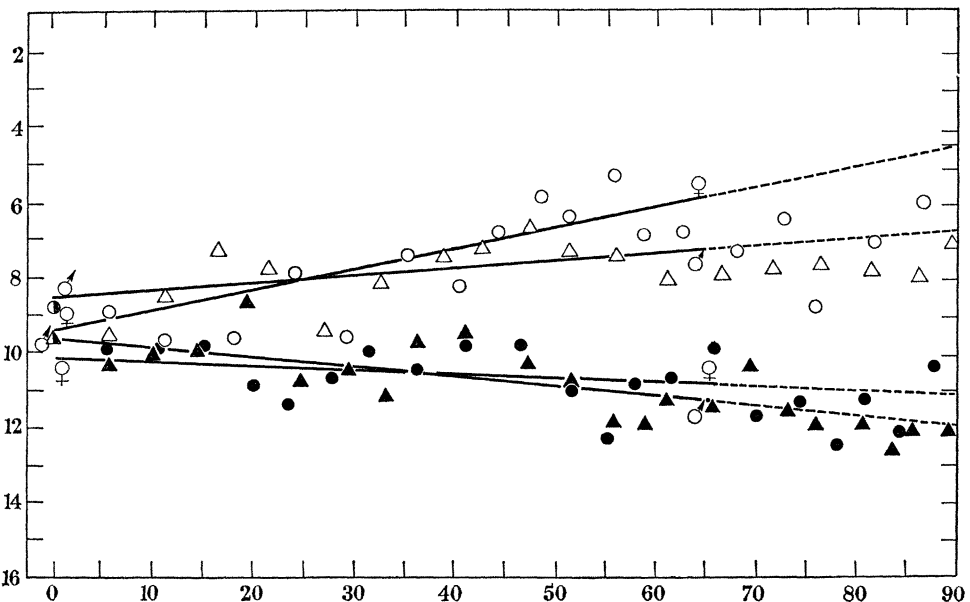


FIGURE 11. The geotactic responses in the populations nos. 13 and 15 plotted in terms of the cumulated selection differentials (abscissa). Other symbols as in figures 9 and 10.

These cumulated selection differentials, due to immigration, are only about half as large as those produced in the same populations by the selection of the non-migrants (see figures 10 and 11). The influence of the migrants on the receiving population can, therefore, be expected to be relatively small. The remarkable fact is, however, that, as shown in table 5, population no. 14 responded in the direction of positive geotaxis in the face of the negative cumulated selection differential; no. 16 did not change appreciably despite the positive selection differential; no. 13 became negatively phototactic contrary to positive selection; no. 15 responded little despite the negative cumulated selection differential.

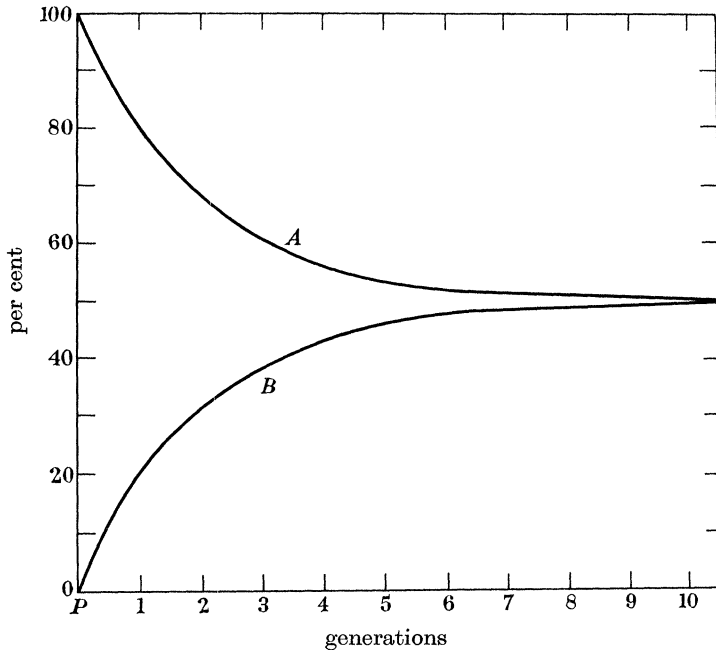


FIGURE 12. The convergence of the genetic composition of populations exchanging 20% of their effective numbers per generation. A population which starts with 100% of *A* and no *B* genes rapidly comes to contain 50% of *A* and *B*.

Calculations of realized heritabilities from these data give negative values, which are biologically meaningless. Evidently the phenotypes of the immigrants did not reflect their genotypes. One more possibility is to suppose that the immigrants, despite their extreme phenotypes, were genotypically like the averages of the donor populations. We may, then, compute the selection differentials as the differences of the means of the donor and the recipient populations, sum them up, and multiply by 0.2. The cumulated selection differentials so obtained are, of course, quite different from those calculated above, namely as follows:

	females	males
geotaxis, population no. 14	+2.50	+3.06
geotaxis, population no. 16	-8.69	-6.89
phototaxis, population no. 13	-4.46	-9.70
phototaxis, population no. 15	+10.72	+10.57

The illusion of negative heritability is thus avoided. The regression lines calculated from these estimates have slopes not statistically different from zero, but their signs are in accord with the changes observed in the recipient populations. What these estimates really mean is that the migrants are genotypically more nearly representative of the averages of the donor populations than their phenotypes might indicate. Since the geotactic or phototactic scores of the donor populations are changing in the directions of the main selection pressures, the genotypic values of the migrants coming from these donor populations change in the same directions, and so do the recipient populations.

#### CORRELATED RESPONSES TO SELECTION

When selection is made for a certain character, such as geotactic or phototactic behaviour, other characters may be changing too, either because they are physiologically correlated with the traits selected, or because the genes which determine them happened to be linked with those for the selected traits in the populations in which the selection was made. The flies which have responded to the selection by becoming positively or negatively photo- or geotactic do not differ in external morphology either from each other or from unselected populations (no extensive biometrical comparisons have, however, been made). A suspicion arose that the positively geotactic flies are either weaker or less active than the negatively geotactic ones, since it would seem that it is easier for a fly to fall downwards than to climb upwards. This suspicion was not confirmed by observations on the speed of the movement of the flies through the maze, or by the vigour of the respective populations.

As stated above in the description of the experimental materials, the populations selected were polymorphic for *AR* and *CH* gene arrangements in the third chromosomes. This polymorphism is balanced, and in populations not selected for either geotaxis or phototaxis equilibria are reached at frequencies between 70 and 80% *AR* and 20 and 30% *CH* (Pavlovsky & Dobzhansky 1966, and references therein). The chromosomal constitution of the selected populations, after 15 or 25 generations of selection, is shown in table 6. All figures are based on samples of 300 chromosomes in 150 individuals.

In populations nos. 18 and 13 the chromosome frequencies are as expected without artificial selection; in nos. 17 and 20 the *AR* are somewhat higher and in no. 14 somewhat lower than expected. The striking deviations are found in nos. 19, 15 and 16, in which *AR* chromosomes are much less frequent than *CH*. Of these populations, nos. 19 and 15 were selected for negative geotaxis; no. 16 was selected for positive phototaxis, while receiving immigrants from no. 15. It appears then, that the selection for negative geotaxis is, in our populations, acting very strongly in favour of *CH* and against *AR* chromosomes. This correlated response is not an invariable property of these chromosomes. Indeed, in the experiments of Dobzhansky & Spassky (1962) exactly opposite effects were observed, i.e. the selection for negative geotaxis favoured *AR*, and the selection for positive geotaxis gave advantage to *CH* chromosomes. Such apparently inconsistent results are perhaps not unusual with correlated selection responses.

Another, and very interesting, correlated response has been discovered by del Solar (1966). He investigated our directional selection lines after 5, and again after 11 generations of selection for positive and for negative geotaxis and phototaxis (populations nos. 17 to 20 in table 6). A moderate, though statistically very significant, preference for homogamic matings was found in all combinations. In other words, the selection for geo- and phototaxis has induced an incipient sexual isolation.

TABLE 6. FREQUENCIES, IN PERCENTAGES, OF *AR* AND *CH* GENE ARRANGEMENTS IN THE THIRD CHROMOSOMES IN THE EXPERIMENTAL POPULATIONS

The initial frequencies were 50 % in all populations

population no. and selection	generation	<i>AR</i>	<i>CH</i>
17. directional, positive geotaxis	15	85.3	14.7
19. directional, negative geotaxis	15	32.0	68.0
18. directional negative phototaxis	15	73.7	26.3
20. directional, positive phototaxis	15	86.3	17.7
13. diversifying, positive geotaxis	25	75.3	24.7
15. diversifying, negative geotaxis	25	15.3	84.7
14. diversifying, negative phototaxis	25	67.7	32.3
16. diversifying, positive phototaxis	25	32.3	67.7

Finally, one may inquire whether the selection for phototaxis has a correlated effect on the geotactic behaviour, and vice versa. In the sixteenth and seventeenth generations of directional selection for phototaxis, populations nos. 18 and 20 were tested for geotactic behaviour with results as follows:

population	geotactic scores	
	females	males
no. 18, photopositive, S-16	10.48 ± 0.23	10.63 ± 0.23
no. 18, photopositive, S-17	11.84 ± 0.24	12.00 ± 0.22
no. 20, photonegative, S-16	7.02 ± 0.17	8.13 ± 0.22
no. 20, photonegative, S-17	8.50 ± 0.19	8.57 ± 0.23

Tests for phototactic behaviour were made in the populations directionally selected for geotaxis, and the following data were obtained:

population	phototactic score	
	females	males
no. 17, geopositive, S-16	9.22 ± 0.18	7.82 ± 0.19
no. 17, geopositive, S-17	8.96 ± 0.16	8.92 ± 0.18
no. 19, geonegative, S-16	8.54 ± 0.17	10.46 ± 0.16
no. 19, geonegative, S-17	9.72 ± 0.16	11.61 ± 0.18

It is evident that the population (no. 18) selected for photopositivity has changed also towards geopositivity, while that selected for photonegativity has remained geotactically neutral. No change in the phototactic behaviour took place in the populations selected to geotaxis as regards females, but the males in no. 19 (geonegative) have seemingly changed in photopositive direction.

The correlated geotactic changes found in the populations selected for photopositivity do not explain the changes which we have observed in the populations

receiving immigrants from the donor populations (see above). Both the phototactic and geotactic records of these donor and receiving populations are known from independent tests.

#### DISCUSSION

Despite the complexity of the experiments described in this paper their results are reasonably clear. The complexity is inevitable because of the low heritability of the behavioural traits which we studied. Yet the same low heritability gives rise in our experiments to certain interesting phenomena which could hardly arise with more ordinary and 'easy' characters. Diversifying (disruptive) selection is applied to pairs of populations which exchange migrants. Under diversifying selection, the populations are selected for both phenotypically extreme expressions of a character (Millicent & Thoday 1961). In our experiments, the diversifying selection is applied however to pairs of populations exchanging migrants, but selected one for phototaxis and the other for geotaxis. We may distinguish the main selection effects caused by the intense selection (40 individuals out of 600) in every generation, and the genetic effects produced by the immigrants in the recipient populations. The immigrants bring to the recipient populations the 'improvements' achieved by the selection in the donor populations. This happens in spite of the fact that the immigrants are selected phenotypically in the direction opposite to that for which the main selection in the donor population is taking place. The low heritability makes it possible for the migrants to transport the genetic changes taking place in the donor populations, despite their own phenotypes failing to reflect these changes. Although the migrants are phenotypically 'inferior' to the mean of the receiving population, they introduce 'superior' genes. 'Inferior' and 'superior' evidently depend, in this context, on the direction in which a given population is changing. Both populations of the pair exchanging migrants thus 'improve' in the same direction, although each of them progresses more rapidly in the direction of the main selective pressure, and more slowly in the direction of the selective pressure introduced by the immigrants.

Genetic processes of the sort observed in our experiments may be imagined to take place also in human populations under social systems which permit or even encourage social mobility (Dobzhansky 1962, pp. 242-252). Such comparisons are evidently hazardous, but we believe that the materials and methods with which we work may be utilized to construct a variety of models which can throw at least some light on the genetics of human societies.

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