
Effects of Selection and Migration on Geotactic and Phototactic Behaviour of *Drosophila*. II

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Effects of selection and migration on geotactic and phototactic behaviour of *Drosophila*. II

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Genetic effects of selection and migration have been studied in populations of *Drosophila pseudoobscura* kept for twenty generations in plastic population cages. The experimental procedure can be seen in figure 1. Four donor populations are selected for positive or for negative phototaxis or geotaxis. The donor populations yield also migrants, which are selected for phenotypes opposite in sign to the selection in the donor populations themselves. The recipient populations are perpetuated by selecting parents with phenotypes close to the average in the respective populations, and adding to them the migrants from the donor populations. The migration is, thus, unidirectional—from the donors to the recipient populations.

The donor populations have, as expected, responded to the directional selection by becoming photo- or geopositive or negative. The recipient populations showed little change for several generations, but eventually changed in the same directions as did the donors. This result seems at first sight paradoxical, because the migrants were selected for phenotypes opposite in sign to the selection in the donor populations. It is shown, however, that the result is explicable when the characteristics concerned have very low heritabilities. The migrants came from genetically improving populations, meaning by 'improvement' simply that these populations were changing in the direction for which they were being selected. Such migrants may transfer genetic improvements even if their own phenotypes do not manifest them.

INTRODUCTION

Experiments described in part I of the present series (Dobzhansky & Spassky 1967) gave some unexpected, and perhaps rather puzzling results. We selected populations of *Drosophila pseudoobscura* for two traits of the behaviour of the flies—the response to light (phototaxis) and the response to gravity (geotaxis). The flies in the starting populations were both phototactically and geotactically neutral on the average. After sixteen generations of selection, positively and negatively phototactic, and positively and negatively geotactic populations were obtained. The realized heritability of both traits was low—8 to 10 % for the phototactic and 2 to 3 % for the geotactic behaviour.

Experiments were then made with two pairs of populations, one population of each pair being selected for phototaxis and the other for geotaxis. Moreover, in every generation the members of a pair exchanged migrants. The migrant individuals were selected for the behaviour opposite in sign to that for which the donor population was selected. Thus, the population selected for positive geotaxis was sending in each generation migrants which evinced the most negative reaction to gravity, and vice versa. The population selected for positive phototaxis was sending migrants which reacted negatively to light, and vice versa (see figure 7 of part I). In agreement with our expectation, the donor populations changed in the

direction in which they were selected; they became positively or negatively phototactic or geotactic, in accordance with the selection applied to them. Also in agreement with the expectation, the immigrants induced genetic changes in the receiving populations. The populations which were selected for geotaxis, and received immigrants selected for phototaxis, changed their reaction not only to gravity but also to light. The direction of the changes was, however, the reverse of what we expected. The population receiving phenotypically photonegative migrants changed slightly but significantly towards photopositivity, that receiving photopositive migrants changed towards photonegativity, etc.

Such results would be hard to explain if the trait involved had a high heritability. As an illustration, suppose that a human population receives immigrants with blue eyes, and sends away emigrants with brown eyes. Though the eye colour in man is not a genetically simple trait, the incidence in the population of persons with blue eyes would surely increase, and that of brown-eyed persons would decrease. The changes which we have actually observed in our experimental populations indicate that the phenotypes of the individuals which we selected as migrants did not accurately reflect their genotypes. This is possible because of the low heritability of the traits involved. The genetic component of the variance of the behaviour of the flies is small.

We wish now to report the results of the experiments which were devised to corroborate those obtained previously, and to test the validity of the explanation suggested. This time we use a less complicated experimental design; instead of pairs of populations which exchange migrants in both directions in every generation, we now have the migration in one direction only. One of the two populations of a pair sends emigrants but receives no immigrants, while the other member of the pair receives immigrants but sends no emigrants. The other simplification is that only the donor population is subjected to a directional selection, while in the receiving population, individuals close to the population mean for phototaxis or for geotaxis are used as parents of the next generation. The experimental populations were started in 1966, and they continue under selection for a different purpose.

THE EXPERIMENTAL POPULATIONS

We have used the same apparatus and the same founder stocks of flies as in the work reported previously (photographs of the apparatus shown in plate 7, facing page 28, in part I). In every generation, groups of between 300 and 350 females or of males from each population were run, the two sexes of course separately, through either the phototaxis or through the geotaxis classification mazes. In about 24 h most of the flies assort themselves among the sixteen terminal vials on the mazes. On the phototaxis maze the vial no. 1 is reached by fifteen dark, and the vial no. 16 by fifteen light passages; on the geotaxis maze the vial no. 1 is the uppermost, and no. 16 the lowermost. The vials nos. 8 and 9 are reached by seven or eight dark and light, or upwards and downwards choices. The mean

phototactic and geotactic scores reported in tables 1 to 4 and in figures 2 to 5 are calculated from the numbers of the flies observed in the terminal vials of the mazes. The mean phototactic score is the average number of choices of light passages, plus one; the mean geotactic score is the average number of choices of downward passages, plus one.

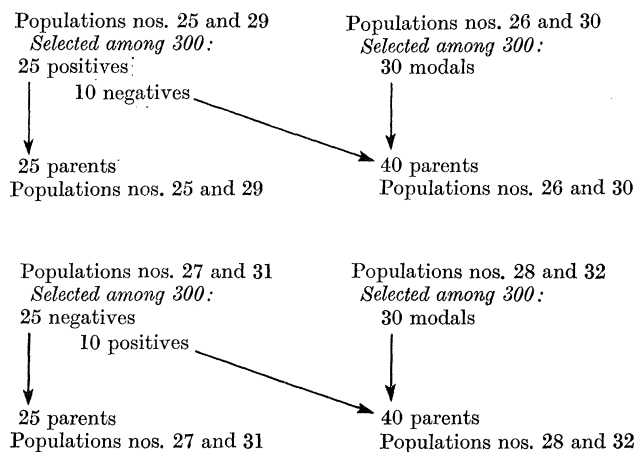


FIGURE 1. The procedure followed in the experiments.

The selections made in the eight experimental populations are indicated in figure 1. The populations nos. 25 and 26, 27 and 28, 29 and 30, 31 and 32 are the pairs in which the odd-numbered population is the donor, and the even-numbered one is the recipient of the migrants. Nos. 25 to 28 are selected for phototactic, and nos. 29 to 32 for geotactic behaviour. In each donor population, twenty-five females and twenty-five males are selected in every generation to be the 'sedentes', i.e. the parents of the next generation. In the same populations, ten females and ten males are selected to be the migrants transferred to the recipient populations. It can be seen in figure 1 that the sedentes and the migrants are always selected in the opposite direction; if the sedentes are positively phototactic or geotactic, the migrants are negative, and vice versa. The positive flies are taken from the vial no. 16, and the negative ones from the vial no. 1, provided that these vials contain the requisite numbers of flies. Otherwise, the positive and the negative flies are taken from two or more vials closest to the positive, or to the negative, end of the maze. In the receiving populations thirty females and thirty males are selected as parents of the next generation, together with the ten pairs of the migrants coming from the donor population. The sedentes in the receiving populations are selected from the terminal vials closest to the population mode, which usually coincides or nearly so with the population mean.

The donor populations are, thus, subjected to a strong directional selection for positive or for negative phototaxis or geotaxis. The selection in the receiving

populations is very weak, and it is, if anything, a stabilizing selection, favouring the mode. The changes that may occur in the receiving populations may safely be ascribed to the immigrants from the donor populations.

All populations were kept in plastic population cages in a constant temperature room at 25 °C; the phototaxis and geotaxis mazes stood in the same room.

RESULTS OF SELECTION IN DONOR POPULATIONS

Tables 1 and 3 report the population mean scores and their variances, as well as the mean scores of the sedentes selected in every generation in the donor populations. The mean scores of the migrants selected for transfer to the recipient populations are reported in tables 2 and 4, together with the mean scores and their variances for the recipient populations. The changes which took place in the populations can be most easily envisaged by inspection of figures 2 to 5. The data for the females and the males are reported separately.

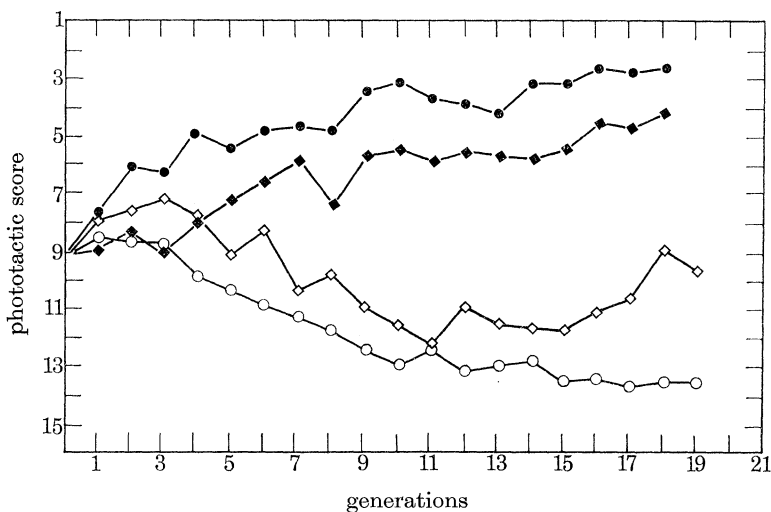


FIGURE 2. Phototactic scores of females in the donor populations nos. 25 (○) and 27 (●), and in the recipient populations nos. 26 (◇) and 28 (◆).

Complete neutrality in the phototactic and geotactic responses would give average scores of 8.5. An average score of 8.5 means that the flies were making equal numbers of light and dark, and downward and upward choices. Both in the experiments reported in part I and in the present ones, the starting populations were neutral or very slightly positive. Table 1 shows that males tend to be more photopositive on the averages than females. In part I it was shown that a slightly greater photopositivity in the males is a fairly general, though not universal, rule for wild populations of both *Drosophila pseudoobscura* and *D. persimilis*.

TABLE 1. SELECTION FOR PHOTOTACTIC RESPONSE IN THE DONOR POPULATIONS, SHOWING THE POPULATION MEANS AND THE MEAN SCORES OF THE SELECTED INDIVIDUALS

generations	females						males					
	positive no. 25			negative no. 27			positive no. 25			negative no. 27		
	mean	σ^2	selected	mean	σ^2	selected	mean	σ^2	selected	mean	σ^2	selected
P	9.04	7.93	13.76	9.04	7.93	3.92	10.96	7.42	15.04	10.96	7.42	5.04
1	8.89	7.52	13.44	7.69	10.22	2.24	10.40	7.79	14.68	9.67	7.49	3.48
2	8.14	6.66	12.60	5.96	7.20	1.56	10.55	6.28	14.88	8.38	8.90	2.68
3	8.88	7.13	13.64	6.16	7.09	1.88	11.53	4.97	15.12	8.83	10.73	2.12
4	9.82	6.94	14.08	4.97	6.22	1.28	12.64	4.48	16.00	7.40	8.58	1.92
5	10.37	5.65	14.24	5.38	7.35	1.12	12.74	5.13	16.00	7.78	10.73	1.48
6	10.88	5.73	14.68	4.86	6.69	1.24	13.47	3.27	16.00	6.34	12.56	1.64
7	11.19	6.22	15.12	4.73	7.04	1.00	12.47	4.44	16.00	6.91	13.73	1.44
8	11.64	6.64	15.52	4.86	8.18	1.00	13.41	3.38	16.00	7.10	13.04	1.48
9	12.35	3.73	15.40	3.32	5.18	1.00	13.78	3.48	16.00	5.30	9.41	1.08
10	12.88	3.46	15.48	3.11	4.16	1.00	14.11	2.77	16.00	6.60	10.92	1.52
11	12.27	2.86	14.96	3.81	5.99	1.00	13.76	3.11	16.00	4.84	9.71	1.00
12	13.06	3.62	16.00	3.89	7.00	1.00	14.32	2.49	16.00	5.57	8.90	1.00
13	12.87	3.51	15.92	4.24	7.64	1.00	14.57	2.15	16.00	5.52	9.96	1.32
14	12.75	4.76	16.00	3.12	4.88	1.00	14.37	2.74	16.00	4.70	8.59	1.00
15	13.32	3.10	16.00	3.13	4.33	1.00	14.63	1.92	16.00	5.54	9.38	1.00
16	13.39	5.67	16.00	2.69	3.01	1.00	14.79	1.90	16.00	5.00	7.57	1.40
17	13.63	3.42	16.00	2.74	3.81	1.00	14.33	4.65	16.00	4.40	8.09	1.00
18	13.59	5.60	16.00	2.64	3.26	1.00	14.39	2.50	16.00	4.45	8.11	1.00
19	13.59	3.24	16.00	2.24	2.92	1.00	14.62	2.01	16.00	4.69	14.72	1.00
20	13.98	2.47	16.00	2.28	2.73	1.00	14.68	3.12	16.00	3.57	5.83	1.00

TABLE 2. PHOTOTACTIC RESPONSE IN THE RECIPIENT POPULATIONS, SHOWING THE POPULATION MEANS AND THE MEAN SCORES OF THE MIGRANTS

generations	females						males					
	no. 26			no. 28			no. 26			no. 28		
	mean	σ^2	migrants	mean	σ^2	migrants	mean	σ^2	migrants	mean	σ^2	migrants
P	9.04	7.93	5.3	9.04	7.93	12.5	10.96	7.42	8.0	10.96	7.42	14.0
1	7.69	8.55	2.3	8.31	7.06	15.2	10.96	6.68	3.6	11.21	6.83	14.7
2	7.48	5.92	2.6	8.26	8.90	12.5	9.69	7.36	3.3	10.78	9.68	14.5
3	6.89	7.89	3.0	8.63	8.41	12.6	9.60	9.09	5.6	11.38	8.52	14.4
4	7.60	7.47	3.7	7.71	6.28	10.4	10.56	7.17	7.8	9.73	7.24	15.7
5	9.05	6.21	4.2	7.12	7.19	11.7	11.57	5.75	7.0	9.42	7.18	14.4
6	8.20	6.85	5.1	6.45	7.89	11.2	12.02	5.26	9.2	9.98	10.33	14.9
7	10.32	5.08	4.7	5.69	8.65	11.1	11.78	5.63	8.1	8.72	11.34	13.9
8	9.64	7.12	5.5	7.49	8.21	11.5	12.34	4.39	9.2	10.32	10.28	14.9
9	10.93	5.29	7.5	5.65	9.27	9.8	12.86	5.07	9.2	9.19	11.06	13.0
10	11.33	5.85	8.2	5.62	8.76	8.9	12.64	4.21	9.5	9.79	10.76	13.6
11	12.13	4.57	8.2	5.74	8.46	10.3	13.33	3.83	9.2	8.59	10.39	11.2
12	10.77	4.87	8.1	5.42	8.40	10.7	13.12	4.03	10.2	8.31	12.17	12.8
13	11.51	5.33	8.2	5.65	8.26	11.3	13.54	3.42	9.9	6.64	13.14	12.6
14	11.81	4.57	7.3	5.74	10.31	9.1	13.35	3.64	9.8	8.45	14.08	12.8
15	11.68	6.38	9.0	5.35	8.67	8.8	13.59	3.37	11.1	9.27	7.35	11.4
16	11.02	5.95	4.8	4.44	7.08	7.6	13.01	3.80	10.8	6.47	10.54	11.6
17	10.75	10.88	8.3	4.59	8.31	8.5	12.83	8.78	5.9	6.56	13.49	11.5
18	8.38	18.75	5.9	4.03	6.78	8.3	12.09	11.22	10.0	6.85	10.96	11.8
19	9.25	14.39	8.8	3.54	4.70	7.6	10.63	14.49	11.1	5.30	8.56	13.4
20	8.28	9.99	8.6	3.69	4.55	7.3	11.56	9.45	7.8	4.49	7.75	11.0

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TABLE 3. SELECTION FOR GEOTACTIC RESPONSE IN THE DONOR POPULATIONS, SHOWING THE POPULATION MEANS AND THE MEAN SCORES OF THE SELECTED INDIVIDUALS

generations	females						males					
	positive no. 29			negative no. 31			positive no. 29			negative no. 31		
	mean	σ^2	selected	mean	σ^2	selected	mean	σ^2	selected	mean	σ^2	selected
P	9.06	17.63	16.0	9.06	17.63	2.33	9.62	16.85	16.0	9.62	16.85	16.0
1	12.23	9.13	16.0	11.34	10.68	5.52	11.66	14.14	16.0	9.37	16.83	16.0
2	10.72	16.89	16.0	10.38	13.66	3.20	11.44	8.21	16.0	9.19	12.42	16.0
3	11.78	14.02	16.0	8.31	15.67	1.72	11.90	8.77	16.0	9.74	9.34	16.0
4	12.55	8.98	16.0	7.92	15.52	1.32	12.43	8.17	16.0	9.85	9.54	16.0
5	12.34	10.65	16.0	7.78	16.40	1.00	12.78	7.90	16.0	9.32	7.61	16.0
6	12.32	11.62	16.0	6.81	15.49	1.12	12.76	6.27	16.0	7.06	19.45	16.0
7	13.09	9.07	16.0	6.88	14.03	1.00	11.43	14.50	16.0	8.69	20.87	16.0
8	12.94	8.26	16.0	6.71	13.72	1.12	12.31	8.90	16.0	7.09	17.65	16.0
9	13.27	10.08	16.0	6.19	14.63	1.00	12.25	10.00	16.0	6.54	19.21	16.0
10	13.72	6.08	16.0	5.98	14.13	1.00	12.71	8.90	16.0	6.88	15.88	16.0
11	13.18	7.14	16.0	4.53	10.43	1.00	13.46	7.14	16.0	5.63	20.19	16.0
12	12.59	8.46	16.0	6.23	11.49	1.08	13.11	6.89	16.0	8.36	14.04	16.0
13	13.25	8.38	16.0	5.59	12.67	1.00	13.56	6.05	16.0	5.30	14.36	16.0
14	13.23	7.94	16.0	4.70	11.57	1.00	12.31	10.57	16.0	6.08	15.30	16.0
15	13.20	8.06	16.0	4.84	13.15	1.00	12.62	9.37	16.0	4.19	10.54	16.0
16	14.07	6.78	16.0	4.04	8.46	1.00	14.28	5.48	16.0	5.14	13.14	16.0
17	13.38	7.23	16.0	4.84	12.03	1.00	12.92	7.35	16.0	5.23	14.72	16.0
18	12.78	11.08	16.0	3.98	11.01	1.00	12.21	10.95	16.0	5.13	16.43	16.0
19	13.23	7.13	16.0	4.39	9.35	1.00	13.20	8.51	16.0	4.81	11.51	16.0
20	13.21	6.70	16.0	4.24	11.10	1.00	13.43	7.47	16.0	6.19	16.07	16.0
21	14.21	5.54	16.0	4.24	9.11	1.00	13.91	5.98	16.0	4.78	12.28	16.0

TABLE 4. GEOTACTIC RESPONSE IN THE RECIPIENT POPULATIONS, SHOWING THE POPULATION MEANS AND THE MEAN SCORES OF THE MIGRANTS

generations	females						males					
	no. 30			no. 32			no. 30			no. 32		
	mean	σ^2	migrants	mean	σ^2	migrants	mean	σ^2	migrants	mean	σ^2	migrants
P	9.06	17.63	3.5	9.06	16.85	15.3	9.62	16.85	3.1	9.62	16.85	15.0
1	11.41	18.48	4.8	11.53	13.06	16.0	11.67	9.21	2.5	10.46	13.20	16.0
2	9.47	17.16	1.5	9.58	16.69	16.0	10.28	8.77	5.8	10.19	10.70	16.0
3	11.05	15.97	1.5	9.89	14.86	16.0	10.83	11.91	5.5	10.56	11.32	16.0
4	10.38	15.58	4.7	8.99	17.27	15.8	11.42	9.82	5.5	10.66	10.24	16.0
5	10.57	18.98	4.1	9.39	15.78	15.6	11.85	8.94	5.0	10.28	8.97	15.9
6	11.30	15.28	3.8	8.93	14.62	15.6	11.64	9.53	6.9	10.80	10.43	16.0
7	11.18	12.44	5.6	8.66	14.47	14.9	11.42	8.76	2.0	8.71	13.76	16.0
8	12.49	10.80	4.7	8.21	14.42	14.4	11.43	10.98	4.5	9.54	14.95	15.8
9	12.22	10.62	3.3	8.17	17.37	14.7	12.10	8.64	5.0	8.97	13.52	16.0
10	12.56	12.38	6.3	8.27	17.29	14.6	12.28	9.07	5.6	9.57	15.31	15.5
11	11.98	9.99	5.1	7.55	14.11	13.6	12.85	10.55	5.7	8.79	14.30	16.0
12	12.78	6.71	4.3	9.56	17.26	14.4	11.53	12.37	6.1	10.74	12.82	15.6
13	13.40	8.17	5.0	9.39	17.53	13.5	12.34	10.80	7.0	8.84	16.80	14.5
14	11.91	10.89	4.7	7.24	20.20	13.7	11.49	12.05	3.4	8.11	20.57	15.3
15	12.61	12.08	4.9	7.49	17.45	14.6	11.70	11.44	4.8	8.17	18.08	12.8
16	12.03	13.73	5.8	7.72	16.25	12.2	11.18	14.23	7.2	8.18	17.78	14.5
17	11.34	14.63	4.8	7.57	16.56	14.3	12.12	9.53	5.8	8.80	16.41	15.7
18	12.39	12.66	2.8	7.46	16.82	13.7	11.77	9.33	3.3	8.03	17.69	15.7
19	12.93	10.11	5.8	7.06	17.20	12.5	12.72	9.09	6.0	7.76	15.30	12.1
20	13.09	9.56	6.8	7.10	16.10	12.6	12.73	8.52	6.3	8.27	15.94	15.2
21	13.61	6.57	6.5	7.60	17.80	14.7	13.81	6.44	7.2	8.50	16.33	14.9

It is evident that all populations have responded to the selection, both in the positive and in the negative directions. After ten generations of selection, the mean phototactic scores were 12.88 in the positive and 3.11 in the negative lines for

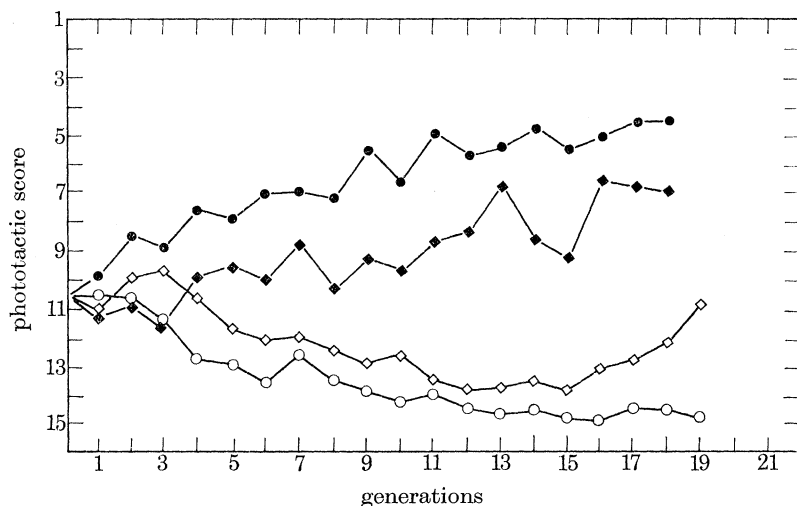


FIGURE 3. Phototactic scores of males in the donor and recipient populations. The meaning of the symbols as in figure 2.

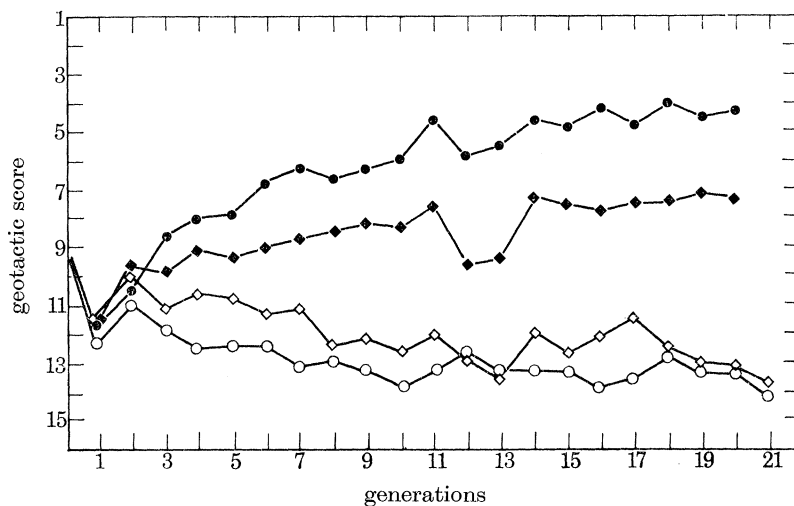


FIGURE 4. Geotactic scores of females in the donor populations nos. 29 (○) and 31 (●), and in the recipient populations nos. 30 (◇) and 32 (◆).

females, 14.11 in the positive and 6.60 in the negative lines for males. The geotactic scores diverged to 13.72 and 5.98 for females, 12.71 and 6.88 for males. Some further divergence took place in the following ten generations. By the twentieth generation, the distribution series of the photopositive and photonegative populations

barely overlap, that is, only few flies from either population enter the terminal vials 7 to 10. With the geopositive and geonegative populations the overlap is considerable even after twenty generations of selection.

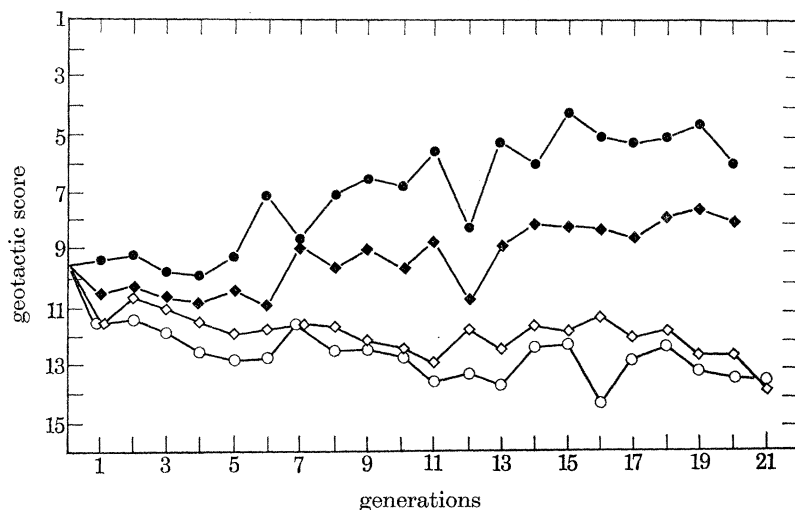


FIGURE 5. Geotactic scores of males in the donor and recipient populations. The meaning of the symbols as in figure 4.

The variances tend to decrease in the selected populations as the selection proceeds. This is, of course, expected if the selection depletes the genetic variability and the variability which is left is environmental in origin. This explanation should nevertheless not be accepted easily, because the ostensible decrease in variance may be at least in part spurious. No fly can make more than fifteen positive or fifteen negative choices in the Hirsch-Hadler classification mazes which we used in our experiments. In the starting photo- and geotactically neutral populations the frequency distributions are generally close to normal and symmetrical; as the means shift towards the positive or the negative ends, the distributions become increasingly more skewed and finally the mode settles in the extreme terminal vials, nos. 1 or 16. That the genetic variance is by no means exhausted even after many generations of selection is attested by the fact that relaxation or reversal of the selection leads to relapse to average geotactic and phototactic neutrality (Dobzhansky & Spassky 1962 and unpublished data).

HERITABILITY

The data in tables 1 and 3 can be utilized to compute the realized heritability for the phototactic and geotactic behaviour. The method of computation devised by Falconer (1955, 1960), and also used in part I was employed again. The selection differentials and responses during only the first twelve generations of selection

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were considered because thereafter the populations tend to reach selection plateaus. The results are shown in table 5, together with the corresponding estimates obtained in our previous work.

TABLE 5. ESTIMATES OF REALIZED HERITABILITY DURING TWELVE GENERATIONS OF SELECTION

	phototaxis		geotaxis	
	old	new	old	new
+ selection ♀♀	0.100 ± 0.009	0.112 ± 0.008	0.032 ± 0.004	0.043 ± 0.010
- selection ♀♀	0.091 ± 0.013	0.090 ± 0.012	0.024 ± 0.011	0.076 ± 0.009
+ selection ♂♂	0.101 ± 0.008	0.113 ± 0.011	0.021 ± 0.007	0.031 ± 0.010
- selection ♂♂	0.076 ± 0.005	0.067 ± 0.008	0.034 ± 0.009	0.054 ± 0.011

The old and the new estimates of the heritability of the phototactic behaviour agree quite well; the new figures for the heritability of the geotactic behaviour are consistently higher than the old ones, although in three out of four comparisons not significantly so. The positive selection for phototaxis seems to show a slightly higher heritability than the negative one, but again scarcely significantly so. The heritability of the response to light is, however, quite consistently higher than that of the response to gravity. The mean heritability, averaging all the figures in table 5, turns out to be 0.0938 for the phototactic and 0.039 for the geotactic behaviour.

As the selection progresses, the realized heritability tends to decline. Estimates of the heritabilities were made separately for the early (1st to 10th) and for the late (11th to 20th) generations of selection. The results are as follows:

population		early	late
no. 25, phototaxis	females	0.107 ± 0.012	0.048 ± 0.008
	males	0.109 ± 0.014	0.039 ± 0.013
no. 27, phototaxis	females	0.121 ± 0.014	0.070 ± 0.018
	males	0.075 ± 0.011	0.049 ± 0.012
no. 29, geotaxis	females	0.089 ± 0.016	-0.001 ± 0.015
	males	0.049 ± 0.017	0.004 ± 0.021
no. 31, geotaxis	females	0.076 ± 0.013	0.043 ± 0.013
	males	0.054 ± 0.012	0.038 ± 0.022

Regression coefficients of heritability on time were also computed; all eight coefficients are negative.

RESULTS IN RECIPIENT POPULATIONS

The mean scores and their variances in the recipient populations are reported in tables 2 and 4, together with the mean scores of the immigrant individuals which entered these populations in each generation. The scores in the recipient and the donor populations can most easily be compared by inspection of figures 2 to 5. All eight experimental populations are descended from the same original one.

Consequently, the starting values are identical in the donors and the recipients as well as in positive and negative selection lines.

The selection for phototaxis is considered first (tables 1 and 2, figures 2 and 3). Population no. 26 (white diamonds in figures 2 and 3) was the recipient of negatively phototactic migrants from the donor population no. 25 (open circles in figures 2 and 3), which itself was selected for positive phototaxis. Conversely, population no. 28 (black diamonds) was receiving positively phototactic immigrants from the donor no. 27 (black circles), which was selected for negative phototaxis. In the first three or four generations the recipient populations seemed to change in the direction in which the immigrants entering them were selected—in figures 2 and 3 the white diamonds are above the black ones for these generations. Thereafter the recipient populations were changing in the same direction as the donors, and hence in the direction contrasting with the phenotype of the migrants. The recipient no. 26 became decidedly more photopositive than no. 28, although the divergence between the two recipient populations always remained smaller than that between the donors.

A similar, though perhaps less striking, situation is observed in the populations selected for geotaxis (tables 3 and 4, figures 4 and 5). Here the mean scores obtained after one generation of selection were accidentally too high, especially for the females. Such sudden rises or drops have been observed from time to time in other tests with the photo- and geotaxis mazes; they are due presumably to some environmental accidents, the nature of which is not known. From the second or the third generation on, the donor populations clearly and consistently diverged in the directions in which they were selected, and the recipient populations followed the donors. Consequently, here too the recipients diverged in the directions opposite to the selection of the immigrants which they received.

Taken at face value, this suggests a negative heritability, which is biologically absurd. A similar appearance of negative heritability was obtained in part I in experiments involving two-way migration. The following analysis was made to discover how this paradoxical result originates. The assumptions underlying the analysis are those commonly made in the theory of quantitative inheritance. It is assumed that the traits are distributed on a continuous scale, and that genetic and environmental components are independent and additive. Furthermore, it is assumed as a first approximation that the heritability of the trait is the same at all stages in the selective process from the first generation to the twelfth.

The calculations may be explained by reference to figure 6, in which is depicted the distribution attained in the donor population after i generations of selection. The mean of the population is equal to h_i . The mean of the recipient population at the same time is f_i , which is less than h_i . Migrants are now taken from the donor population as depicted in the figure, the mean of the migrant population being e_i , which lies below f_i . The actual genetic contribution of the migrants is, however, not equal to e_i , but lies much closer to the mean of the population h_i . By the usual theory, the mean contribution of migrants is assumed to be g_i , where $(h_i - g_i)$ is

equal to $(h_i - e_i)$ multiplied by the heritability, h^2 . As drawn in the figure, and as usually was the case after a few generations in all recipient populations, g_i is greater than f_i . Thus the effect of the migrants is to raise the mean value of the trait in the recipient population. This may at first sight seem paradoxical, since the actual phenotypic value of the migrants is below the mean value of the recipient population. The low heritability of the traits in question is responsible for the fact that the migrants are on the average genetically above, but phenotypically below, the mean of the recipient population.

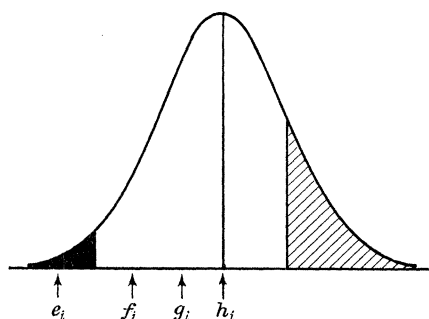


FIGURE 6. Distribution of phototactic or geotactic scores in the donor populations after i generations of selection; the sedentes hatched, the migrants black; other explanations in text.

The actual values expected in the recipient populations are derived under the assumption that the contribution of the migrants to the recipient populations is proportional to their numbers. This may be an approximation, since it has been shown by Petit & Ehrman (1969) that the genetic contribution of the rare type, the migrants in this case, is often greater than would be expected from their numbers, owing to an advantage possessed by the rare males in mating. Since in all cases the new recipient populations were started with thirty pairs close to the mean of the previous generation in the recipient populations, and ten pairs of migrants from the donor populations, the expected mean of the new generation in the recipient populations was calculated as $\frac{3}{4}f_i + \frac{1}{4}g_i$.

Before the calculations of expectations in the recipient populations were undertaken, it was found convenient to replace the actual observed points in the donor populations, viz. the h_i , by the expected points from the heritability analysis described previously. This smoothed out some of the large random fluctuations. It also allowed a more accurate estimate to be made of the likely initial value, which was taken as the intercept of the regression line with the zero generation point, a method which leads to some complications which will be described later.

The calculations were carried out recursively. The mean of a recipient population in the initial generation, f_0 , was taken as the same value as the donor population, h_0 . The expected mean in the first generation was then calculated using the values f_0 , and the observed values e_0 and h_0 , although as described above the

actual values used for h_0 , h_1 , etc., were not the observed values but rather the replacements from the linear regression. Likewise in the second generation the expected value f_1 and the observed values e_1 and h_1 were used, and so on. In this way the expected values $f_1 \dots f_{12}$ were calculated recursively, without ever using the interim observed values in the recipient population.

The resulting expected curves for the four recipient populations are all shaped very similarly. There is a small initial drop in the populations in which the donor populations are selected upwards, and a rise in the populations selected downwards. After the initial period however, the expected values of the recipient populations followed behind those of the donor populations. The results are illustrated in figure 7 for the recipient populations nos. 26 and 28 selected for phototaxis, and in figure 8 for nos. 30 and 32 selected for geotaxis. The values given are those for the females, the results for the males from the same populations are essentially similar.

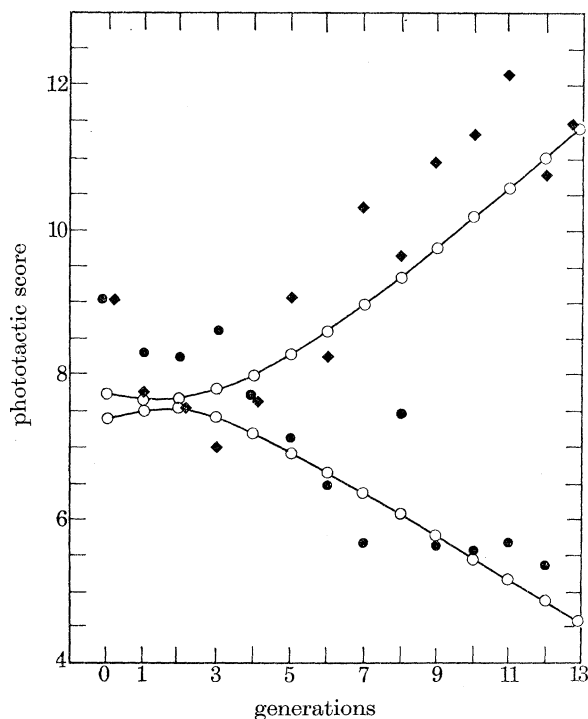


FIGURE 7. Expected (○—○) and observed values for the females in the recipient populations no. 26 (◆) and no. 28 (●). Selection for phototaxis.

In most cases, the trends in the recipient populations appeared to be close to the expected, despite a considerable scatter of points. Unfortunately, it is difficult to devise any test of the goodness of fit of the expected lines. However, one way in which it seems possible to tell whether the expected values consistently underestimate or overestimate the observed value is to combine the values from all

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populations. For this calculation the data for the populations which were selected downwards are artificially replaced by the complements of the observed values, viz. 17 minus the observed values. The means of the observed and expected values are then calculated for each generation, and the results are shown in figure 9. Considerable caution must, of course, be taken in the interpretation of this figure, since it involves the pooling of points whose expected values are similar but not identical.

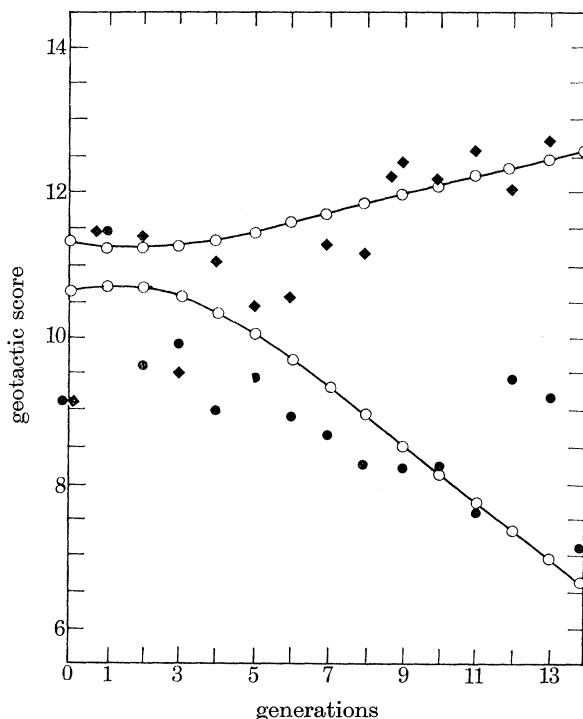


FIGURE 8. Expected (○—○) and observed values for the females in the recipient populations no. 30 (◆) and no. 32 (●). Selection for geotaxis.

It appears that the values in the receiving populations follow quite closely the predicted values, with the exception of the initial few generations. An explanation of this discrepancy is, however, readily available. If the values in the donor populations are not in fact linear, but instead have a tendency towards some asymptote, then it is readily seen that the linear regression line which replaces the points will give a value which in the initial generations is less extreme than the true value, i.e. lower for the populations being selected in an upwards direction. Such a situation is expected in the donor population if the heritability decreases during the course of the experiments. This could be due either to the genetic variability being partially depleted, or to the increased opposition of natural selection to the artificial selection. As described above, generation by generation heritabilities were

calculated for the populations, and it was found that in all cases the heritability fell on the average over the course of the experiment.

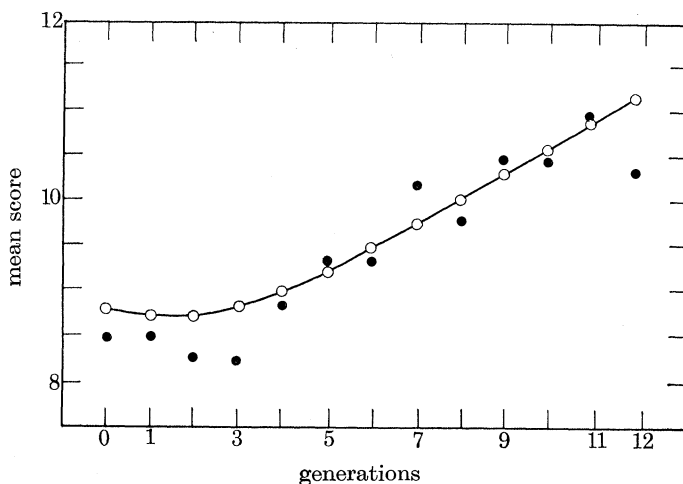


FIGURE 9. Averages for expected (○—○) and observed values (●) in all recipient populations; data for females and males combined.

DISCUSSION

The experiments described above are similar in principle to those reported in part I. The plan of the newer experiments has, however, been made simpler than that of the older ones. We have studied pairs of experimental populations of *Drosophila pseudoobscura* which were selected for their response to light (phototaxis) or to gravity (geotaxis). In the older experiments the two populations of a pair exchanged migrants; in the newer experiments the migration is unidirectional, one population serving as the donor and the other the recipient. Moreover, in the newer experiments only the donors are subjected to directional selection, either for phototaxis or for geotaxis. The recipient populations are perpetuated by selecting groups of flies of mean phototactic, or geotactic, scores close to the means of these populations themselves; to these are added the migrants transferred from the donors, and selected for phenotypes opposite in sign to the direction of the selection in the donor populations. The results of both series of experiments are in agreement with each other. The migrants bring about genetic changes in the receiving populations. The interest centres on the direction of these changes. The migrants are always selected for phenotypes opposite in sign to what the donor populations are selected. Nevertheless, these phenotypic 'discards' transfer genetic 'improvements' to the receiving populations. 'Improvement' means in this context a change in the direction of which the selection operates in donor populations. Analysis of the data shows that this, at first sight paradoxical result, is in agreement with the expectation. The heritability of the responses to light and to

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gravity is low, and individuals from genetically improving populations are genetically superior to those in the receiving populations, even if the phenotypes of the migrants do not manifest the superiority. This may well be relevant for assessment of possible genetic consequences of migration in human populations. We hope to discuss this subject in another publication, in connexion with other experiments now under way.

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