

STUDIES ON NATURAL POPULATIONS OF DROSOPHILA. II.  
HERITABILITY AND RESPONSE TO SELECTION FOR WING LENGTH  
IN DROSOPHILA MELANOGASTER AND D. SIMULANS  
AT DIFFERENT TEMPERATURES

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SELECTION under different environmental conditions varying in nutrition or temperature poses a problem to be solved on sound genetical grounds. The problem is whether the best response to selection can be achieved when selection is carried out under optimal conditions or when it is carried out in some other environment that is especially favourable for the expression of genes affecting the desired trait. Most selection experiments, on *Drosophila*, have been carried out under optimal conditions; for recent references see LATTER and ROBERTSON (1962).

The existence of genotype-environment interaction may mean that the "best" genotype in one environment is not the best in another environment. Evidence is accumulating that such interaction is common (PARSONS 1959; ROBERTSON 1960a; for more general references see HULL and GOWE 1962).

The situation is important in breeding policy and raises two problems: (a) To what extent is the response to selection which is achieved in one environment also expressed in another environment? (b) Does the attenuation in the heritability resulting from genotype-environment interaction interfere seriously with the response to selection?

Actually, the problem is much broader than expressed here. Natural populations and also domesticated species inhabit many environments and, therefore, several environments have to be taken into account when selecting (see DICKERSON 1962 for a good discussion of the problem).

The present experiments were carried out to examine the response to selection for wing length in *Drosophila melanogaster* and *D. simulans* at different temperature conditions. In particular, the effects of temperature on the response to selection as well as on the heritability of wing length were studied by transferring the selected lines from one temperature to another. Observations were taken on other traits to determine their correlated responses, if any.

EXPERIMENTAL PROCEDURE

*The initial foundation populations:* One population of *Drosophila melanogaster* and one of *D. simulans* were the basis of the present experiments. These populations were derived from flies captured at the University of Alexandria Farm. For locality and technique for crosses, and also

for maintenance of the initial populations for the experimental work, see TANTAWY and MALLAH (1961).

The absolute means for wing and thorax length for both males and females in both species of *Drosophila* at 18°, 24° and 28°C, and their respective coefficients of variation are presented in Table 1.

The results indicate clearly that both sexes in *D. melanogaster* are significantly longer in wing length, but not for thorax length, at each temperature than in *D. simulans*. Males and females, in both species, have different mean sizes, but they show nearly the same coefficient of variation for wing and thorax length, although the former character is almost twice as long as the latter. There is a gradation in size; wing and thorax length are longer at 18°C and decrease gradually with the increase of temperature. These results are in good agreement with those reported by TANTAWY and MALLAH (1961) working on the same two species.

*Mating system and selection procedure:* Each selected line was started by measuring 60 pairs of flies in three sublines A, B and C and the selected flies were mated in a cyclical system of mating (ROBERTSON and REEVE 1952) to minimize inbreeding inevitable in the outbred selected lines. In other words, three largest selected pairs for wing length (plus direct'on) in each subline were used, whereby in each generation the three selected males from subline A were mated to the three selected females of subline B which gave offspring denoted A; selected males from B mated with females of C give offspring denoted B and selected males of C mated with females of A gave offspring denoted C and so on for every generation. The same procedure was followed in case of the short-wing selected lines, where the three smallest flies were selected from each subline and mated as before.

In each of the two species and at each temperature of 18° and 28°C, one line was selected for long wing length and the other for short wing length. The technique used for the maintaining different selected lines was exactly the same as that described by ROBERTSON and REEVE (1952). Selection for long and short wings was carried out for 25 generations at each temperature for both species, except in the case of short wing selected line in *D. simulans* at 28°, where only 17 generations of selection were completed.

After 20 generations of selection at either temperature, in both species, new lines were taken off the high (28°C) and the low (18°C) temperature lines, and selected for a further five generations at the other temperature as well as at 24°. The original selected lines were also maintained so that we can compare the effects of change of temperature on selection response after many generations of selection.

Control stocks from each of the two species were maintained in mass mating at the different temperatures and given the same treatments as the selected lines.

TABLE 1

*Morphological differences between males and females of D. melanogaster and D. simulans in mean wing length and thorax length, at different temperatures with their respective coefficients of variation (C.V.%)*

Temperature	<i>D. melanogaster</i>				<i>D. simulans</i>			
	Wing length		Thorax length		Wing length		Thorax length	
	Mean	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
<b>Males</b>								
18°C	201.81	2.47	96.26	2.40	184.23	2.38	95.62	2.53
24°C	180.15	1.98	93.19	2.36	175.43	2.14	92.14	2.32
28°C	166.83	2.46	87.35	2.47	159.52	2.73	85.92	2.69
<b>Females</b>								
18°C	227.26	2.51	106.54	2.17	203.34	2.43	106.52	2.52
24°C	204.56	2.03	103.18	1.84	200.42	2.05	102.62	2.08
28°C	193.17	2.41	99.87	2.43	181.23	2.76	98.05	2.75

Units of measurement are 1/100 mm. Each mean was taken from 100 flies.

*Relaxed lines:* Relaxation of selection was effected by allowing 20 pairs of flies, picked at random in a given generation, to mate and lay eggs together. Selection was relaxed in all the selected lines after the 5th, 10th, 15th and the 20th generations for five successive generations. In each case, five vials were set up on the same days as their original selected lines, and five pairs of flies were measured from each vial on the same days as in the selected and control lines.

*Heritability estimates.* 1. *The initial foundation populations:* For the estimation of the heritability for wing and thorax length in both species at 18°, 24° and 28°C, five progeny tests were carried out in each species at each temperature, three of which were mated at random and the other two were mated assortatively. The regression of offspring on midparent was applied throughout the present analyses, since this method provides the most accurate estimates for heritability (ROBERTSON and REEVE 1952). The parents of each progeny test and their progeny were carried out under similar temperature. The technique for the maintenance of the progeny tests was essentially the same as that reported by TANTAWY (1959).

2. *Selected lines:* Heritability was similarly estimated after the 5th, 10th, 15th, 20th and 25th generations in all the selected lines. At these generations, other progeny tests were carried out, by taking samples from the original selected line at a given temperature and rearing them at the reverse one. Heritability was also estimated in each of the relaxed selected lines at each temperature after five generations of relaxation.

*Other characters:* In each generation throughout the experimental work, records were kept for thorax length, number of eggs cultured and the number of adults hatched, to study the response to selection for wing length on thorax length and the change in the percentage of emergence in the various selected lines.

## RESULTS

*Heritability of wing length in the initial populations:* The results of each progeny test and the weighted means, at different temperatures, are presented in Table 2. Heritability estimates resulting from the assortative matings were

TABLE 2

*Heritability of wing length in the initial foundation populations at different temperatures*

Progeny No.	Mating system	18°C		24°C		28°C	
		$h^2$	No. of matings	$h^2$	No. of matings	$h^2$	No. of matings
a. <i>D. melanogaster</i>							
1st	Random	32.21 ± 3.89	97	35.21 ± 4.10	100	25.13 ± 4.21	100
2nd	Random	34.23 ± 3.33	100	38.91 ± 2.95	100	23.29 ± 3.48	95
3rd	Random	30.98 ± 4.14	100	37.82 ± 3.88	100	24.05 ± 3.62	90
4th	Assortative	31.64 ± 3.98	95	39.18 ± 3.02	98	30.51 ± 4.11	98
5th	Assortative	30.39 ± 4.91	100	40.25 ± 3.21	97	28.42 ± 3.59	99
Totals and weighted means		31.91	492	39.27	495	25.48	482
b. <i>D. simulans</i>							
1st	Random	25.41 ± 5.56	100	30.34 ± 4.32	100	21.41 ± 5.06	98
2nd	Random	28.31 ± 4.34	98	29.95 ± 3.81	100	23.91 ± 6.41	91
3rd	Random	25.40 ± 5.68	95	32.81 ± 3.45	98	27.84 ± 5.01	95
4th	Assortative	24.33 ± 6.01	100	28.99 ± 4.45	100	22.44 ± 5.88	95
5th	Assortative	26.82 ± 6.72	100	34.81 ± 4.21	100	21.41 ± 6.13	95
Totals and weighted means		26.29	493	31.74	498	23.44	474

corrected for the magnified variance between parents, as suggested by REEVE (1953). The results for wing length ( $h^2$  for thorax length is not included since it behaves in almost the same manner as wing length) indicate clearly that natural populations of *D. melanogaster* and *D. simulans* possess a considerable amount of genetic variability due to the additive gene effects. The population of *D. melanogaster* displays a higher percentage of heritability estimate, in every progeny test, than does *D. simulans*, and this is true at each temperature. The differences between species are significant ( $P < 0.01$ ).

The weighted means for the heritability estimates at 24°C are about 39 percent and 32 percent, in populations of *D. melanogaster* and *D. simulans*, respectively. Both estimates decline at lower and higher temperatures to 31.9 and 26.3 percent at 18°, and to 25.5 and 23.4 percent at the high temperature, respectively. Thus the populations of the two species differ in their genetic variance for wing length and may also differ in the relative reduction of the heritability estimates at more extreme temperature conditions. The reduction in the heritability estimates may represent genotype-environment interaction. Such evidence for genotype-environment interaction at lower and higher temperatures is in good agreement with that reported by TANTAWY (1961) on populations of *D. pseudoobscura*. The heritability estimates at 24° do not differ very much from those given by TANTAWY (1959) on other populations of *D. melanogaster*.

The results of the genetic correlation between wing and thorax length in both species, as estimated by HAZEL's (1943) formula for random matings and REEVE's (1953) formula for assortative matings, are presented in Table 3. The genetic correlation is high at 24°C and declines in both species at lower and higher temperatures. The decrease at high temperature is more pronounced than that at the low temperature. At either extreme temperature the genetic correlation between wing and thorax length in *D. melanogaster* shows less reduction than in *D. simulans*.

*Response to selection. a. Changes in wing length:* Since heritability estimates show high values for the additive genetic variance, one would expect effective selection in directions of long and short wing selected lines. This was found to be the case in both species; the results for wing length (sexes averaged) are presented in Figure 1, as percentage deviation from controls. These results illustrate

TABLE 3

*Genetic correlation between wing and thorax length at different temperatures*

Progeny No.	<i>D. melanogaster</i>			<i>D. simulans</i>		
	18°C	24°C	28°C	18°C	24°C	28°C
1st	0.8084	0.8239	0.7889	0.7588	0.7888	0.7507
2nd	0.8095	0.7988	0.8008	0.8089	0.8109	0.7444
3rd	0.7581	0.7881	0.7411	0.7850	0.8183	0.7608
4th	0.7896	0.8009	0.7356	0.7503	0.7882	0.7332
5th	0.8052	0.8236	0.7585	0.7436	0.7947	0.7468
Means	0.7941	0.8071	0.7649	0.7693	0.8002	0.7472

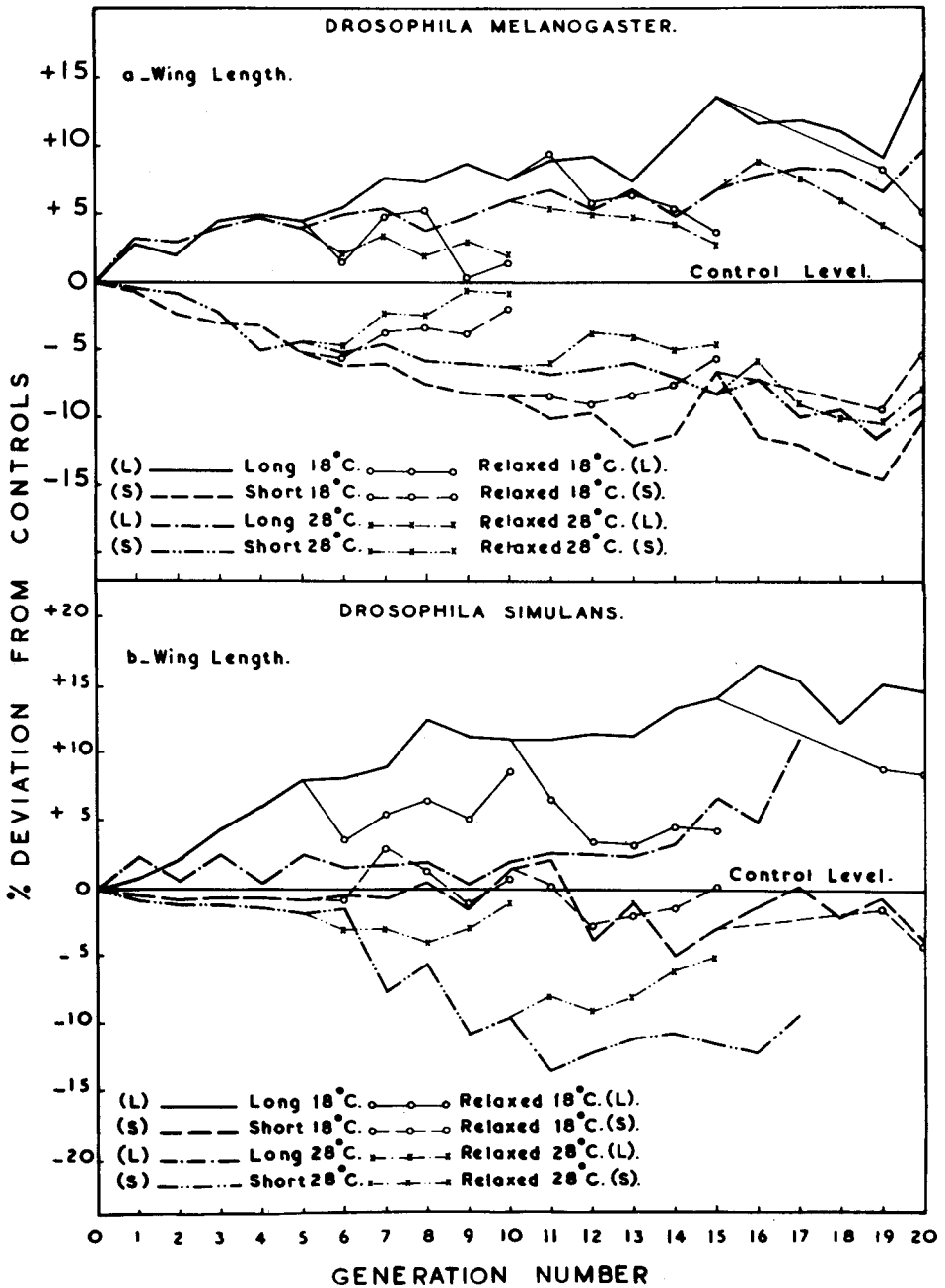


FIGURE 1.—Percentage deviations of wing length (sexes averaged) from controls at different temperatures.

clearly that selection is effective in both species at both temperatures; short wing selected lines show more response to selection than long, apart from the lines of *D. simulans* selected at 18°C, where the line selected for long wings shows more response than that for short.

Comparing the response to selection at different temperatures within the same species, one notices that in *D. melanogaster*, selection is more effective at 18°C, in both directions, than in lines selected at 28°. Selection at 18° is also more effective in the long wing selected lines in *D. simulans*, but at 28° selection for short wing is relatively more effective. The behaviour of thorax length was similar to that found in wing length, indicating high genetic correlation between them (Table 3).

The divergence between the long wing and the short wing selected lines at the two temperatures, in both species, increases gradually from generation to generation at each temperature; *D. melanogaster* shows more divergence between the selected lines. The divergence is greater between lines selected at 18°C than between those selected at 28°, while between the long and short wing selected lines in all series, at the reverse temperature after the 20th generation, it shows a decrease compared with that found in the original selected lines for the same generations. Table 4 shows the divergence between long and short wing lines from Generation 21 to Generation 25 for the selected character under the original

TABLE 4

*Average differences between plus and minus lines for wing length (as percentage deviations from controls) when selected at different temperatures, after the 20th generation of selection for five successive generations*

Generation	Selected originally at 18°C	Selected originally at 18°C and transferred to		Selected originally at 28°C	Selected originally at 28°C and transferred to		
		24°C	28°C		24°C	18°C	
<b>a. <i>D. melanogaster</i></b>							
21	25.24	24.03	21.81*	17.55	13.21*	17.36	
22	29.35	22.97*	22.70**	20.87	13.65**	18.20*	
23	26.72	25.24	24.99	20.45	14.77**	17.46*	
24	29.90	23.39*	24.05*	22.13	14.90**	18.31*	
25	37.31	26.77***	23.20***	20.30	13.13**	16.83*	
Average	29.70	24.48	23.35	20.26	13.93	17.63	
<b>b. <i>D. simulans</i></b>							
21	17.91	13.21*	10.91**	14.02	11.77***	3.29***	
22	18.79	13.09**	9.13***	14.95	14.47***	5.80***	
23	20.48	14.00**	9.94***	18.22	15.66***	10.87***	
24	20.85	15.91**	10.53***	17.18	16.79***	6.65***	
25	22.74	17.96**	16.16**	20.40	15.03***	2.65***	
Average	20.15	18.54	11.33	16.95	14.74	5.85	

Test of significance for the differences in the divergence between the selected lines at the original temperature and that at the reverse one:

- \* Significant at the level of P<0.05.
- \*\* Significant at the level of P<0.01.
- \*\*\* Significant at the level of P<0.001.

temperature and the reverse one. The response to selection is expressed to a lesser degree in the new environmental conditions, and both species show a significant decrease.

Although the same character was selected in *D. melanogaster* and *D. simulans* under exactly the same environmental conditions, the response to selection differed in the two species.

b. *Relaxed lines*: Selection was relaxed in all the selected lines, after every five generations of selection for five successive generations. Figure 1 also shows the results as percentage deviations from controls. The results show that relaxation in the earlier generations of selection causes wing length to return almost to the level of the unselected populations. In the later generations of selection, the relaxed lines returned about half way to the control level. Similar phenomena were observed by ROBERTSON and REEVE (1952), REEVE and ROBERTSON (1953), by TANTAWY (1956), all working on body size in *D. melanogaster*.

c. *Phenotypic variation*: Phenotypic variability in all the selected lines at each temperature is calculated as coefficients of variation, and the results are presented in Figure 2 for wing length of both species. The phenotypic variability of the lines selected at different temperatures behaves differently. At 18°C, the variance of long and short wing selected lines declines in both species, though insignificantly so compared with the control populations. At 28°, the situation is different; selected lines show higher variability than the controls, and in both species short wing lines show higher variability than long wing lines.

The relaxed selected lines (Figure 2) show an increase in their phenotypic variation as compared with their original selected lines. When the original environmental conditions for the selected lines are changed to either high or low temperature, the phenotypic variance increases under the new temperature of 28°C and decreases at 18°C. Thus, the selected lines for long and short wing length in *D. melanogaster* at 18°C show the values (presented as averages for 21 to 25 generations) of 1.84 percent and 2.57 percent for the two selected lines. These coefficients were increased to 3.05 percent and 2.92 percent, respectively, when selected lines were transferred to 28°. On the other hand, selected lines at 28° show values of 2.75 and 2.21 percent, respectively. These values were decreased to 2.01 and 1.89 percent when selected lines were maintained at 18°. Selected lines in *D. simulans*, at both temperatures, behaved in a similar manner as that reported in *Drosophila melanogaster*.

*Changes in the heritability estimates*: It has been reported (Table 2) that the initial foundation populations of *D. melanogaster* and *D. simulans* carry a great deal of genetic variance, with the former species showing higher heritability than the latter, extremes of temperature causing a decline in both species. In the lines selected at 18° and 28°C for both directions in both species, heritability of wing length was estimated every five generations before and after relaxation. The results are given in Tables 5 and 6 for both the selected and relaxed lines. These indicate that selection at either temperature leads to an apparent increase in the heritability estimates, even though the selection response has ceased in long wing lines, and in all cases short wing lines display greater variance than long. Relaxa-

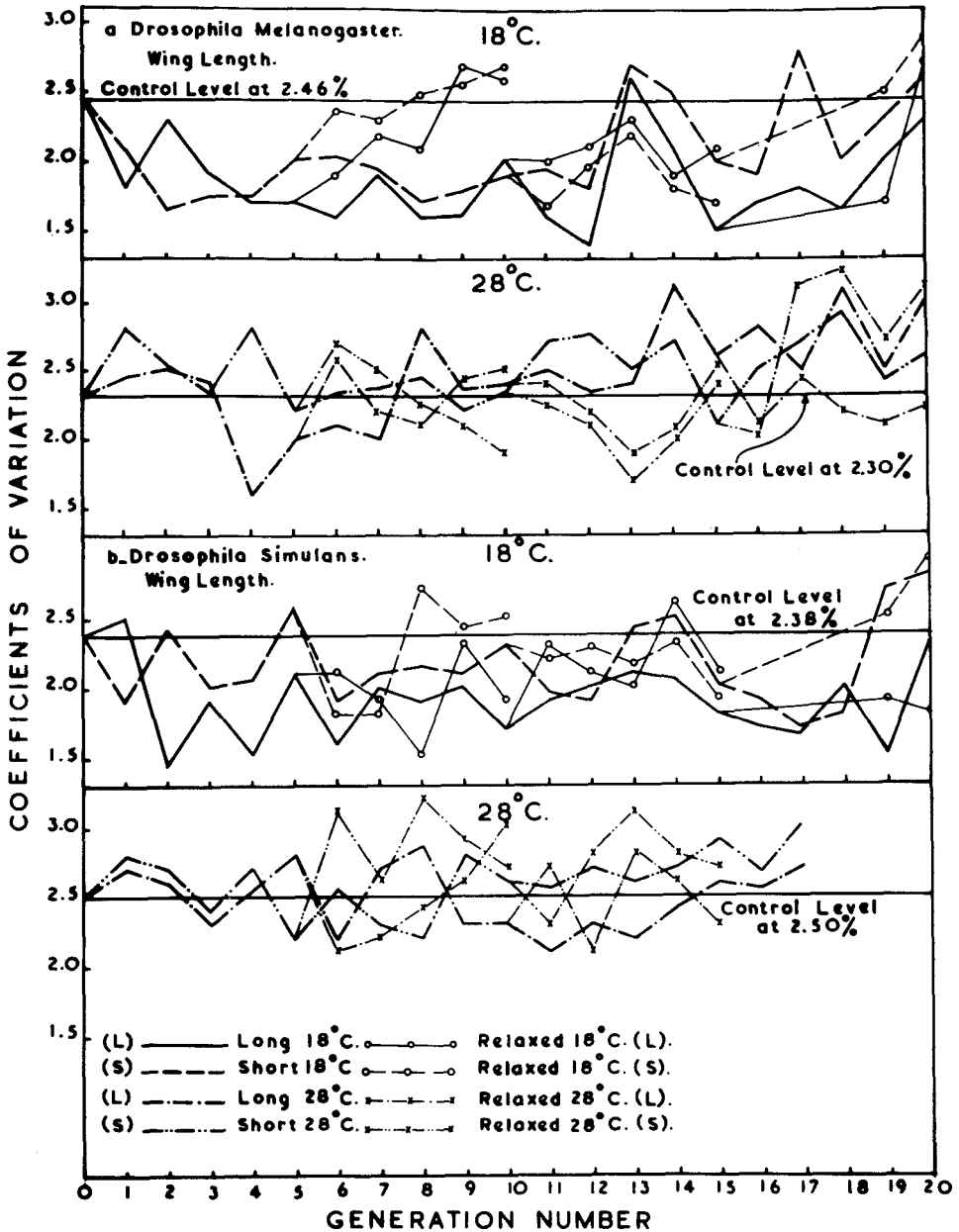


FIGURE 2.—Coefficients of variation for wing length (sexes averaged) at different temperatures.



TABLE 5

*Heritability estimates (percent) for wing length in the selected lines at different temperatures*

Generation	18°C		28°C	
	Long	Short	Long	Short
<b>a. <i>D. melanogaster</i></b>				
5	35.31 ± 8.11	42.30 ± 5.91	26.53 ± 7.62	27.11 ± 6.73
10	39.32 ± 4.51	45.29 ± 6.07	27.66 ± 8.31	30.72 ± 6.33
15	40.95 ± 6.22	50.67 ± 7.11	31.73 ± 9.27	38.15 ± 8.11
20	43.21 ± 7.30	48.85 ± 6.20	34.56 ± 8.13	40.11 ± 8.23
25	45.56 ± 7.09	43.91 ± 7.00	38.05 ± 10.21	39.40 ± 8.92
<b>b. <i>D. simulans</i></b>				
5	26.31 ± 5.34	31.22 ± 5.11	23.51 ± 6.21	25.13 ± 5.31
10	26.82 ± 6.20	34.31 ± 6.71	20.31 ± 5.92	30.22 ± 6.72
15	30.01 ± 5.91	37.33 ± 6.21	26.57 ± 7.32	29.51 ± 5.67
20	32.14 ± 6.71	35.05 ± 7.84	25.33 ± 8.32	31.64 ± 6.11
25	34.22 ± 7.01	39.56 ± 5.23	27.68 ± 7.54	32.83 ± 8.32

tion of selection causes a decrease in the heritability estimates in the selected lines.

The effects on heritability were also considered of reversing the temperature, compared with the heritability found under the original temperature (Table 5) at which the lines were selected. Table 7 shows the results for the various progeny tests carried out in each selected line. When the genetic variance is calculated under the new environment heritability declines at 18° and increases at 28°C.

Alteration of the genetic variance of body size by changing the environment was noticed by TANTAWY (1961) in populations of *D. pseudoobscura*.

*Effects on survival to adulthood:* The percentage of eggs yielding adult flies for all the selected lines are shown in Figure 3. Selection in both directions at each

TABLE 6

*Heritability estimates (percent) for wing length in the selected lines after relaxation of selection for five successive generations*

Generation	18°C		28°C	
	Long	Short	Long	Short
<b>a. <i>D. melanogaster</i></b>				
5	33.25 ± 5.62	35.53 ± 8.12	28.13 ± 5.61	30.00 ± 5.62
10	35.95 ± 8.11	27.05 ± 7.09	20.54 ± 8.92	29.21 ± 6.71
15	34.01 ± 7.23	31.77 ± 6.23	25.34 ± 5.67	31.22 ± 8.92
20	36.52 ± 8.29	39.82 ± 4.52	24.01 ± 7.11	30.92 ± 5.09
25	32.89 ± 6.67	38.09 ± 8.23	28.92 ± 8.21	34.05 ± 7.14
<b>b. <i>D. simulans</i></b>				
5	23.11 ± 4.56	28.13 ± 5.01	20.21 ± 6.11	23.56 ± 5.31
10	24.95 ± 8.11	29.00 ± 6.87	18.13 ± 7.23	25.11 ± 6.71
15	20.56 ± 7.23	30.19 ± 5.33	25.32 ± 6.98	26.09 ± 8.09
20	28.56 ± 5.23	28.05 ± 8.21	21.02 ± 8.91	24.22 ± 7.22
25	25.31 ± 8.01	31.43 ± 6.62	23.92 ± 8.84	28.56 ± 6.76

TABLE 7

*Heritability estimates (percent) in the selected lines for wing length after reversing the original temperature to the reverse ones*

Generation	Lines selected at 18° and progeny tests for $h^2$ at 28°C		Lines selected at 28° and progeny tests for $h^2$ at 18°C	
	Long	Short	Long	Short
<b>a. <i>D. melanogaster</i></b>				
5	28.52 ± 8.66	30.14 ± 7.11	31.51 ± 7.15	33.56 ± 8.91
10	29.31 ± 5.71	31.44 ± 8.22	35.23 ± 6.21	32.71 ± 7.32
15	30.13 ± 6.99	29.56 ± 6.57	32.07 ± 5.27	37.51 ± 6.20
20	25.47 ± 8.32	31.82 ± 6.32	29.27 ± 5.58	36.54 ± 6.09
25	27.23 ± 8.99	28.82 ± 7.75	30.11 ± 5.97	38.88 ± 5.08
<b>b. <i>D. simulans</i></b>				
5	22.13 ± 5.13	24.51 ± 6.09	25.56 ± 6.21	30.52 ± 6.92
10	20.19 ± 6.72	26.39 ± 6.31	27.31 ± 7.11	29.62 ± 5.11
15	18.37 ± 8.93	25.21 ± 5.02	28.41 ± 8.00	29.98 ± 7.08
20	24.13 ± 5.94	27.92 ± 7.93	27.94 ± 7.65	31.84 ± 7.14
25	25.10 ± 5.72	30.11 ± 6.98	31.10 ± 6.87	34.85 ± 7.86

temperature causes reduction in the percentage of survival to adulthood of both species as compared with the controls. At each temperature, lines selected for long wings show a higher percentage of emergence than lines selected for short wings. This is true for all the selected lines apart from tests at 28°C in *D. simulans*, where the short wing line shows a higher percentage of emergence, compared with long wing line at the same temperature. The relaxed lines, in the earlier generations, show an increase in the percentage of emergence over the control level, while at the later generations of selection this character shows a slight increase in the direction of the controls, in agreement with the results reported by different workers in selection experiments.

In all the selected lines, a temperature shift downward leads to an increase in percentage emergence, while an upward shift leads to a decrease. Thus, the lines selected for long and short wing length during Generations 21 to 25 show at 18°C (values are based on averages for five generations) the values of 45.42 and 37.84 percent; these decreased to 29.23 and 28.06 percent, respectively, when the selected lines were transferred to 28°. On the other hand, selected lines at 28° showed the values of 26.91 percent for long wing and 39.71 percent for short wing; these increased to 41.67 and 66.69 percent, respectively, when lines were transferred to 18°. Similar results were found in selected lines of *D. simulans*, although emergence was lower.

#### CONCLUSIONS

In the present experiments, long-term two-way selection for wing length in *Drosophila melanogaster* and *D. simulans* was carried out to study the response to selection in both species, at two different temperatures, 18° and 28°C. Changes in the genetic variability of wing length were also studied in the course of selec-

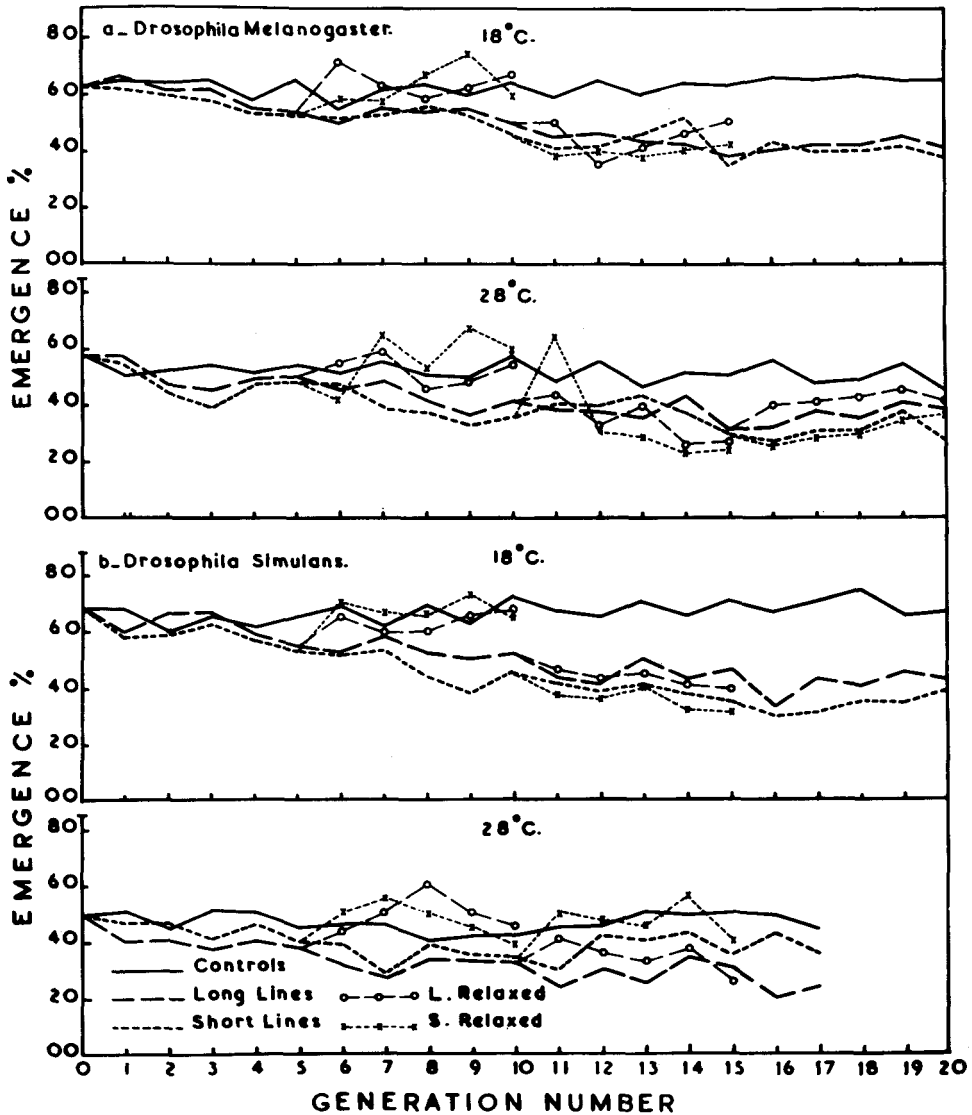


FIGURE 3.—Percentage of emergence (eggs to adults) in the selected lines at different temperatures.

tion for 25 generations at one temperature, and also at the reverse temperature from Generations 21 to 25.

Selection is effective in both species at both temperatures; *D. melanogaster* shows more response. Such differences in the response to selection between species could be attributed to the higher heritability in the initial foundation population of *D. melanogaster* and in *D. simulans* (Table 2). However, the higher value of the heritability estimate at 18°C is also consistent with the greater response to

selection at this temperature than at 28. These results confirm those reported on selection experiments carried out by different workers, e.g. DRUGER (1962).

The deviation from controls (Table 4) declines significantly in most of the selected lines, when the original temperature under which the selected lines were maintained for long generations, was changed either from 18° to 28°C or *vice versa*.

Similar results were reported by DRUGER (1962), who selected for wing length in *D. pseudoobscura* at two different temperatures. He explained his differences in carry-over of selection effects as the result of different growth processes being selected for, which would not contribute to growth to the same extent in the two environments. He further stated that "if these processes do not contribute to the character (i.e. wing length) to the same extent in other environments, selection for larger or shorter wings may at first involve processes which show little carry-over; as selection continues other underlying mechanisms which show good carry-over may become selected for, or *vice-versa*".

The general increase in the heritability estimates in all the selected lines may be explained on the hypothesis that selection, at either temperature, favors more heterozygous individuals as parents of next generation (REEVE and ROBERTSON 1953). Therefore, the selected lines may be characterized by a relatively high phenotypic variance, and relaxation of selection may cause an increase in variability towards the control level, particularly in the earlier generations, and a decrease in the heritability estimate almost to the initial foundation populations. The long wing selected lines in the present work show exactly the same behaviour as that described by ROBERTSON and REEVE (1952) and REEVE and ROBERTSON (1953), but the short wing lines behave differently. They found that lines selected for short wing length responded neither to forward nor backward selection and had a heritability of zero. Such differences between the present experiment and those of the previous authors may be due to the fact that our short wing lines have not reached the same stage as had those of ROBERTSON and REEVE, since ours are still responding to selection.

From the evidence of the heritability estimates, in lines originally selected at 18° or 28°C, and then selected at the reverse temperature, whereupon the genetic variance declines (Tables 5 and 7; Generation 25), one may conclude that the reduction in the additive genetic variance is higher at 28° than at 18°. Therefore, the decline in the heritability estimates from changing temperature is due to the increase of environmental variation as well as to environment-genotype interaction under the new conditions. Additive genetic variance of a given trait may be affected more by changing temperature from warm to cold, rather than the reverse. Similar results were reported by TANTAWY (1961) on populations of *D. pseudoobscura*.

The present results should be considered along with the observations of ROBERTSON (1960b), who in describing the results of selection in *Drosophila* on different diets stated that "selection on a high plane of nutrition has so far led to the greater absolute response to selection for large body size, but the difference due to selection is not maintained when the animals are grown on a low plane. Also, differ-

ences produced by selection on a poor diet are proportionally less when the diet is improved, while adaptation to the low plane conditions may reduce the possibility of increasing body size by further selection under better conditions".

Finally, one may conclude from the present results that the expression of the genetic makeup for a given individual under good constant environmental conditions differs from that under less favorable ones. A superior genotype in one environment could not be expected to show the same superiority in another environment. Therefore, it is apparent that selection should be carried out under environmental conditions similar to those in which selected lines are to be maintained. Such a conclusion is in agreement with those of FALCONER (1960) on mice and ROBERTSON (1960a,b,c,) on *Drosophila*.

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#### SUMMARY

The effects of selection for wing length in natural populations of *Drosophila melanogaster* and *D. simulans* were studied at 18° and 28°C. Two lines were selected in each species at each temperature, one for long and the other for short wing length. Heritability estimates were carried out in the initial foundation populations and at intervals of five generations before and after relaxation of selection. At the 20th generation, selected lines were transferred to the reverse temperature and selection was carried out for another five generations. Heritability of wing length was estimated in each of the selected lines, at Generations 21 to 25.

Heritability estimates indicate that both populations carry considerable genetic variability. Such estimates were 38.27 percent for *D. melanogaster* and 31.74 percent for *D. simulans*, at 24°. At higher and lower temperatures, heritability estimates were 31.91 and 26.29 percent (18°C), and 25.48 and 23.44 percent (28°C).

The initial foundation populations show a high genetic correlation between wing length and thorax length, 0.80 in both species at 24°; this value tends to be lower at higher and lower temperatures.

Selection was effective in both species at both temperatures; short wing selected lines show usually more response than long ones. The response to selection is more pronounced in *D. melanogaster* than in *D. simulans*, and in all lines selection is more effective at 18° than at 28°.

The limits of selection are reached earlier at 28° than at 18°.

At 28°, selection causes an increase in the phenotypic variation of the selected lines over that found in the control populations, while at 18° there is an insignificant decline.

Both relaxing selection and changing the temperature cause a reduction in the heritability estimates for wing length. The response to selection is also decreased when the temperature is changed.

Selection causes a reduction in the survival to adulthood in all the selected lines; the decline is greater at 28° than at 18°.

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