STUDIES IN QUANTITATIVE INHERITANCE IN DROSOPHILA

By

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CONTENTS

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II. List of Publications

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TANTAWY, A. O., 1956 Response to selection for wing length in Drosophila melanogaster with different systems of mating. Genetica, 28: 231 - 262.

TANTAWY, A. O., 1957 Genetic variance of random inbred lines of Drosophila melanogaster in relation to coefficients of inbreeding. Genetics, 42 : 121 - 136.

TANTAWY, A. O., 1957 Heterosis and genetic variance in hybrids between inbred lines of Drosophila melanogaster in relation to the level of homozygosity. Genetics, 42 : 535 - 543.

TANTAWY, A. O., 1959 Selection limits with sib matings in Drosophila melanogaster. Genetics, 44 : 287 - 295.

TANTAWY, A. O., and M. O. VETUKHIV, 1960 Effects of size on fecundity, longevity and viability in populations of Drosophila pseudoobscura. Amer. Naturalist, 94 : 394 - 404.

TANTAWY, A. O., 1961 Effects of temperature on productivity and genetic variance of body size in Drosophila pseudoobscura. Genetics, 46 : 227 - 238.

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TANTAWY, A. O., and G. S. MALLAH, 1961 Studies on natural populations of Drosophila. I. Heat resistance and geographical variation in Drosophila melanogaster and D. simulans. Evolution, 15 : 1 - 14.

TANTAWY, A. O., G. S. MALLAH and H. R. TEWFIK, 1964 Studies on natural populations of Drosophila. II. Heritability and response to selection for wing length in Drosophila melanogaster and D. simulans at different temperatures. Genetics, 49 : 935 - 948.

TANTAWY, A. O., 1964 Studies on natural populations of Drosophila. III. Morphological and genetical differences in wing length of Drosophila melanogaster and D. simulans in relation to seasonal fluctuations. Evolution, 18: (In Press).

TANTAWY, A. O., and F. A. RAKHA, 1964 Studies on natural populations of Drosophila. IV. Genetic variances of and correlations between four characters in Drosophila melanogaster and D. simulans. Genetics, 49: (IN Press).

TANTAWY, A. O., and M. R. El-HELW, Studies on natural populations of Drosophila. V. Correlated response to selection in Drosophila melanogaster. Genet. Res., (Sent for publication).

III. PUBLICATIONS

1. Selection for long and short wing length in *Drosophila melanogaster* with different systems of mating. Genetica, 28 : 231 - 262. (1956).

Genetica 28 (1956): 231—262

SELECTION FOR LONG AND SHORT WING LENGTH IN DROSOPHILA MELANOGASTER WITH DIFFERENT SYSTEMS OF MATING

by

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CONTENTS

I. INTRODUCTION

The extent to which artificial selection can lead to change in different characters is of considerable theoretical and practical interest. Where selection produces an initial change, followed by a change in the response, as observed in many experiments as shown by MATHER and HARRISON (1949), ROBERTSON and REEVE (1952), REEVE and ROBERTSON (1953), RASMUSON (1955) and others, only detailed analysis can demonstrate the cause of the limitation. Naturally there is no single explanation and each case must be considered separately.

Explanation generally falls under the following headings:

a. Loss of genetic variability.

b. Adverse changes in viability or fertility which are correlated with selected characters.

c. Selection of heterozygotes.

It is obvious that the general level of genetic variability must have a great influence on the possible response to selection. A good deal of the selection experiments with *Drosophila*,especially the earlier work, MACDOWELL (1915 and 1917), MAY (1917), STURTEVENT (1918), PAYNE (1918 and 1920), ZELLENY (1922) and ZELLENY and MATTOON (1915), involved close inbreeding i.e. brother — sister matings. Responses to selection were comparatively slight, and more recent work by SISMANIDIS (1942), RASMUSON (1949 and 1952) and TANTAWY (1953 and 1956) are consistent with these earlier experiments.

However, where the mating system has been such to minimize the effects of inbreeding inevitable with small populations, response to selection have been much greater and sustained over many generations. Thus MATHER (1941 and 1942), MATHER and HARRISON (1949) and RASMUSON (1955), working on abdominal bristles, REEVE (1952), ROBERTSON and REEVE (1952) and REEVE and ROBERTSON (1953) working on body size, were able to produce considerable changes, which nevertheless ceased or became extremely gradual after a number of generations.

Inbreeding at random with brother-sister matings from an unselected population usually caused a decline of wing and thorax length of *Drosophila* as demonstrated by ROBERTSON and REEVE (1952) and TANTAWY (1956) and accompanied with decrease in genetic variances of such charatcers particularly at the higher levels of inbreeding, TANTA-

WY (1952). The F_1 of the crossed inbred lines exceeded that of the mid-parent level as shown by ROBERTSON (1954), ROBERTSON and REEVE (1955*a* and *b*) and generally genetic variance in such crossed inbred lines rised almost to the control level, TANTAWY (unpublished).

Since there does not appear to have been any systematic attempts to study the effects of the different levels of the genetic variability on response to selection, the present experiments were desgined to provide some information on this point. Selection for long and short wing length has been carried out using two different mating systems which provide various intensities of inbreeding. These are achieved by mating in successive generations between double-first cousins or by using a special cyclical mating scheme which reduces inbreeding intensity to a low level. A comparison will be made between the results obtained from the previous mentioned systems and those reported by TANTAWY (1956) who used brother-sister matings, selecting for the same characters.

II. TECHNICAL PROCEDURE

1. *Material and culture methods*

The stock used in the present experiments is *Drosophila melanogaster* (Crianlarich stock) which has been kept in mass matings in large populations. The absolute means of wing and thorax length with their respective coefficient of variation (C.V.) for such a stock reared under $25.0° \pm 0.50$ are presented in Table 1, (units of measurements are of 0.01 mm).

TABLE 1. *Mean size of wing and thorax length in the initial population with their respective coefficients of variation*

Item	Wing length		Thorax length	
	Males	Females	Males	Females
Mean size	182.97	212.94	93.57	109.97
C.V.	2.33	2.41	2.89	3.03

It is clearly shown that males and females have different mean size for wing and thorax length, but they show nearly the same coefficient of variation although the former character is almost twice as long as the latter.

Wing and thorax length were measured by an instrument devised by ROBERTSON and REEVE (1952) and the procedure in the present experiments to control the environmental variation, and collection of eggs were adopted after them.

2. *Mating system and selection procedure*

Two different systems of mating were used in maintaining the various selected lines. These systems are: double–first cousins and out-breeding matings. In case of brother–sister matings as reported by TANTAWY (1956), and as shown in Figure 1*a*, two individuals were used every generation. Thus male A was mated to female B to produce the individuals of the next generation in which all of them are full brothers and sisters, Then male A′ was mated to female B′ to obtain the next generation and so on throughout the experiment where these mated individuals are the largest flies in the long wing selected line and the smallest flies in the short wing selected line.

In the case of double–first cousin matings, Figure 1*b*, four individuals were used every generation, where F and H are brother and sister, the

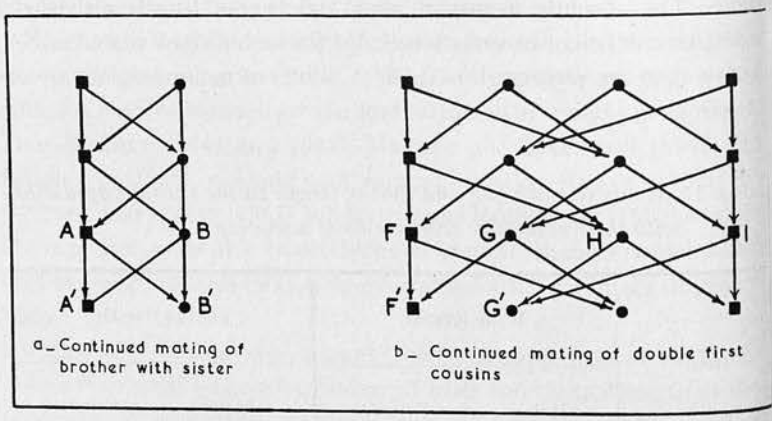

Fig. 1. Diagram illustrating continued matings between,

a) Brothers and sisters, and

b) Double–first cousins.

same relationship exists between G and I. The relationship between F and G, H and I which are mated individuals are double–first cousins. This mating procedure was continued in every generation and selection was practised in both directions as in the case of brother–sister matings

The outbreeding system used in the present experiments has been explained by ROBERTSON and REEVE (1952) to minimize inbreeding inevitable in the selected outbred lines. Each selected outbred line was started by measuring sixty pairs of flies in three groups A, B, and C and the three largest pairs in each group were selected. A cyclical system of mating was used whereby in each generation male A is mated to female B gives offspring denoted A, male B mated with female C gives offspring denoted B and male C mated with female A gives offspring denoted C. This system was carried out throughout the experiment where the three extreme males and females from each of A, B and C sublines were mated together to form the new separate lines. The decrease in percentage of heterozygosity in such type of mating is very low as reported by REEVE (1952) and ROBERTSON and REEVE (1952).

In the case of different intensities of inbreeding, WRIGHT (1921) has applied the path coefficient method to estimate the rate at which heterozygosity is reduced in different systems of mating and it is possible to calculate how many generations must elapse before the same degree of homozygosity is attained. Thus with brother–sister and double–first cousin matings, 25% of the original heterozygous loci will be homozygous after the first and the third generations respectively.

In the case of brother–sister matings 50% and 75% coeffiicents of inbreeding will be arrived at the third and the sixth generations respectively, and in the case of double–first cousins the same degree of homozygosity will be attained at the eigth and the sixteenth generations respectively.

In each system of mating used in the present experiments two lines have been maintained, one line was selected for long wing and the other for short wing. In each of these lines, twenty pairs of males and virgin females (measured on two successive days, ten pairs of each sex on each day) were measured, and six selected pairs were set up assortatively. The flies were selected on the basis of their deviations from the vial mean rather than their absolute size. These matings were fed for three days, then transformed to oviposition vials for egg counts and selection. Cultures containing the usual cornmeal–molasses–agar

medium, fortified with additional dried baker's yeast and well yeast with live yeast, were set up for these eggs from which these selecte matings were maintained. Only the largest matings in the long wi selected lines and the smallest matings in the short wing selected lin were used for selection for the next generation. The other matings we set up as safety matings to be used if the first mating did not breed.

In each generation a control stock was maintained in mass matin under the same environmental conditions. Four vials were used t culture eggs (not more than 70 eggs in each vial) each day on the sam four days as the selected lines. Five pairs of flies were measured fro each vial cultured on the first two days.

Records have been kept from the beginning of the experiment fo the number of eggs cultured in each vial and the number of adul emerging in all different lines and for the control stock.

3. *Relaxing selection*

The relaxed selection lines to be described were maintained b allowing twenty pairs of flies, picked at random at a particular genera tion, to mate and lay eggs together. Selection was relaxed at abou 25%, 50% and 75% coefficients of inbreeding in the case of double first cousin matings and at the fifth, tenth and fifteenth generations i the case of outbreeding matings, for five successive generations. I each case four vials were set up on the same four days as the selecte lines, and five pairs of flies were measured from each vial of the firs two days.

4. *Heritability estimates*

a. The initial stock

To estimate the heritability of body size, i.e. wing and thorax length in the initial foundation population, three progeny tests have bee made, two of which were mated at random and the other wa mated assortatively. In the case of random mated progeny tests five vials were collected from the mass mated original stock, and after emergence virgin females were separated from males. Twenty pairs of flies were measured from each vial and then mated at random in pairs giving all together one hundred pairs. Each pair was left in a well yeasted vial for feeding and mating for three successive days, then transferred into oviposition vials for collecting eggs. Eggs were cultured

in vials and after emergence ten pairs of flies were measured from each mating set up on the first two days, giving all together ten hundred pairs, to provide an estimate of the average size of the progeny of each mating.

In the heritability estimates with assortative matings, the procedure was essentially the same as in the random mating except that instead of the random mating of the parents, the matings were between the largest male X largest female, second largest male X second largest female and so on.

b. The selected lines

Heritability was estimated in the case of double–first cousin matings at about 25%, 50% and 75% coefficients of inbreeding. At these levels heritability estimates were carried out in the following way: from each of the selected line, twenty pairs of flies were measured and mated assortatively, fed for three days and then transferred into oviposition vials for the collection of eggs which were introduced into cultures over four successive days. Five females were measured from each of the cultures of eggs produced by each mating on the first two days.

In the case of outbreeding matings, heritability was estimated at the fifth, tenth, and fifteenth generations. The general procedure for the structure of heritability was the same as estimated at the different levels of inbreeding.

III. RESULTS

1. *Heritability of wing and thorax length and the genetic correlation between them in the initial population*

Three estimates of the heritability of body size, i.e. wing and thorax length, were carried out in the initial foundation population and the regression method, as described by LUSH (1949), was used. Two of these estimates involved random matings and the other assortative matings, the latter being corrected for the magnified variance between the parents as suggested by REEVE (1953).

The results are set out in Table 2.

TABLE 2. *Heritability of wing and thorax length and the genetic correlation between them in the initial population*

Test	Type of mating	Heritability %		D.F.	Genetic correlation %
		Wing	Thorax		
1st.	Random	41 ± 4	46 ± 5	98	84
2nd.	Random	47 ± 4	48 ± 3	98	78
3rd.	Assortative	45 ± 6	47 ± 6	98	83

The weighted means for all tests indicate that nearly 45% and 47% of the total variance for wing and thorax length respectively, are due apparently to additive gene effects. Heritability estimates clearly demonstrate the presence of abundant genetic variance for both characters in the initial stock. These estimates are, however, much higher than those reported for the same characters on another stock of *Drosophila melanogaster* by REEVE and ROBERTSON (1953) and by TANTAWY (1952, 1954 and 1956).

Genetic correlation between wing and thorax length was calculated in the first two tests by HAZEL's formulae (1943) and in the third test by REEVE's formulae (1953). After correcting for the magnified variance between the parents in the third test, the average genetic correlation was found to be 81.7%, indicating a highly positive estimate between the two characters.

TANTAWY (1952) and REEVE and ROBERTSON (1953) reported an average genetic correlation of 74% between wing and thorax length of the Nettlebed unselected stock which is lower than that obtained from the present study.

2. *Effects of selection*

a. Changes of wing length

The effects of selection in the experimental lines are measured as percentage deviations from the control stock. As both sexes show almost the same general trend, their percentage deviations have been averaged as shown in Figure 2*a* and *b* for double–first cousin and outbreeding systems fo mating respectively.

The results as presented in Figure 2 and as shown by TANTAWY (1956) in the case of brother–sister matings, clearly demonstrate that

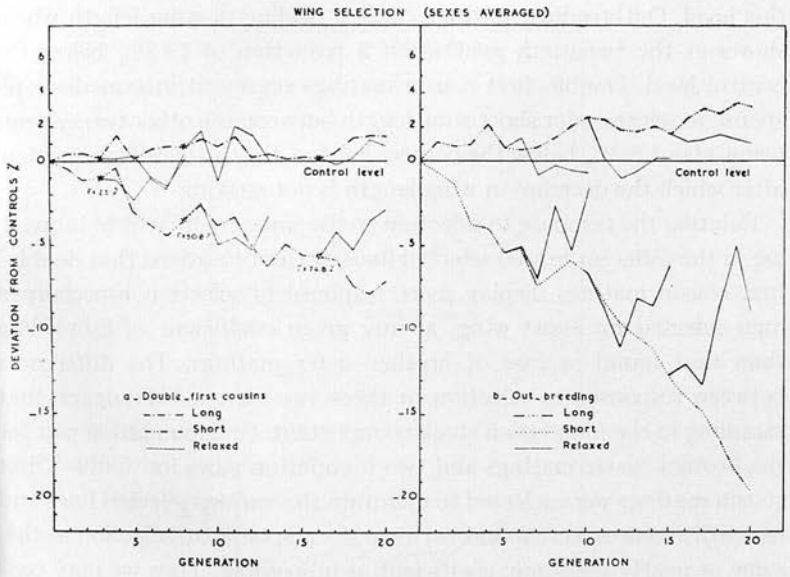

Fig. 2. Percentage deviations of wing length from controls in the case of,
a) Double–first cousins, and
b) Outbreeding matings.

selection has been effective in all the systems in both directions, i.e. long and short wing length. Short wing selected lines show higher response to selection than long wing selected ones. The line selected for long wing in the case of double–first cousins increases gradually from the first generation of selection to the nineth, where it shows an increase of about 1.5% over the control level, after which response to selection is not steady. The outbreeding matings show an increase of about 3% in wing length at the end of the experiment. Matings between brothers and sisters show less response to selection than the other systems. TANTAWY (1956) reported that selection with sib matings was effective to the third generation in both directions, after which the selected lines remained almost constant. They showed an increase of 1.2% and 2.9% over the control level in both selected lines for long wing length. The second percentage , i.e. 2.9%, is very high and could be due to gene recombination.

Short wing selected lines with brother–sister matings showed at the third generation 1.32% and 1.67% below the control level in both selected lines, after which they remained almost constant in size at

this level. Outbreeding matings cause a decline in wing length whi shows at the twentieth generation a reduction of 19.5% below t control level. Double–first cousin matings represent intermediate r sponse to selection for short wing length between the other two syste being about 6.3% below the control level at the thirteenth generati after which the decrease in wing length is not striking.

Relating the response to selection to the same coefficient of inbree ing in the different inbred selected lines, it can be noticed that doubl first cousin matings display more response to selection, especially lines selected for short wing, at any given coefficient of inbreedi than that found in case of brother–sister matings. The differen between responses to selection in these two systems do suggest th sampling in the foundation stock is important. One foundation pair f the brother–sister matings and two foundation pairs for double -fir cousin matings were selected to maintain the various selected lines a hence differences were found between the responses to selection at th same or nearly the same, coefficient of inbreeding. Thus we may co clude that the results obtained in any inbreeding experiments wi selection depend, primarily, on the genetic constitution of the found tion animals that were inbred.

The behaviour of thorax length (results are not included) in t different selected lines shows a striking resemblance to that for wi length, due to the high genetic correlation between them.

Divergence of wing length between high and low lines in the case double–first cousins increases gradually from the first generation selection to the thirteenth as shown in Figure 3*a*, after which the div gence fluctuates. In the case of thorax legnth, Figure 3*b*, such div gence remains almost constant between the seventh and the fifteen generations, after which there is a slight increase to the end of t experiment. The outbred selected lines show a steady increase in su divergence in both characters from the first generation of selection the end of the experiment. In the case of brother–sister such divergen for wing length, TANTAWY (1956), stabilized at about the third gener tion of selection.

Although the same characters were used for selection, with vario systems of mating being carried out, selection showed different r sponses. From the previous results responses to selection could be pr sented as:

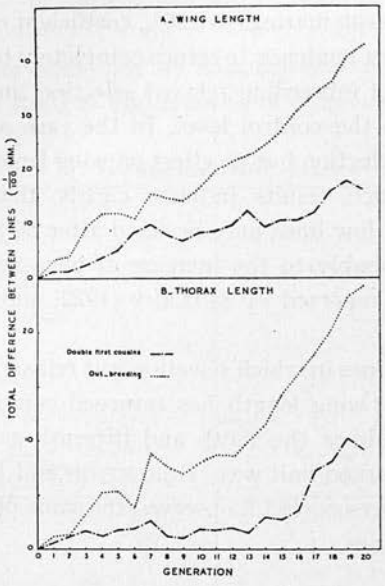

Fig. 3. Divergence of long and short wing selected lines. (Sexes averaged) *a*) Wing length, and
b) Thorax length.

a. Limits of selection arrived at the third generation of inbreeding, i.e. at about 50% coefficient of inbreeding in case of brother–sister matings.

b. Such limits could be arrived at the thirteenth generation, i.e. at about 67.6% coefficient of inbreeding in case of double–first cousin matings.

c. In case of outbreeding matings such limits of selection are not yet achieved, although these selected lines are carried out for twenty generations.

b. Effects of relaxing selection

The relaxed selection tests throw some light on the genetic changes of the different selected lines, but limited assistance made it difficult to carry the relaxed selection lines further than five successive generations.

The effects of relaxing selection in the inbred selected lines on wing length at different coefficients of inbreeding are presented in Figure 2*a*

for double–first cousin matings. At 25% coefficient of inbreeding, suc selected lines have a tendency to return completely to the control leve At higher levels of inbreeding relaxed selection lines tend to retu back half way to the control level. In the case of brother – siste matings relaxed selection has no effect on wing length at higher level of inbreeding. Such results indicate clearly that the differenc between high and low lines may be fixed after 50% coefficient of in breeding, due probably to the increase of homozygosity. The sam results have been reported by ZELLENY (1922) and RASMUSON (19 and 1952).

In the outbred lines in which selection was relaxed at the fifth gen ration, Figure 2*b*, wing length has returned completely to the u selected level, while at the tenth and fifteenth generations relax selection lines returned half way. ROBERTSON and REEVE (1952) an REEVE and ROBERTSON (1953) observed the same phenomena in the selected outbred lines.

c. Phenotypic variability

Phenotypic variability of wing length in all the selected lines studi are calculated as coefficient of variation in order to minimize th effects of change of mean size on variance. It is found that males an females have nearly the same coefficient of variation, although th difference between their mean size is about 15% as shown in Table

Coefficients of variation for all the selected lines are presented i Figure 4*a* and *b* for the double–first cousin and outbreeding systems mating respectively (the values represent tht average between the tw sexes), and only the average level of the controls is shown since the variance did not show any marked trend.

TANTAWY (1956) had shown that inbreeding with brother–siste matings caused a decrease in the variability of high and low lines i the third generation, after which it remained almost constant. Thes results clearly indicate that this type of mating is accompanied by decrease in phenotypic variability of the selected character, due pr bably to the decrease of genetic variance within lines. When selectio was relaxed in these lines, at higher rates of inbreeding, relaxed sele tion has no effect on the variability and the coefficient of variatio remained well below the control level. These results confirm what ha

been achieved on body size by showing that genes affecting wing length have been fixed at higher levels of inbreeding.

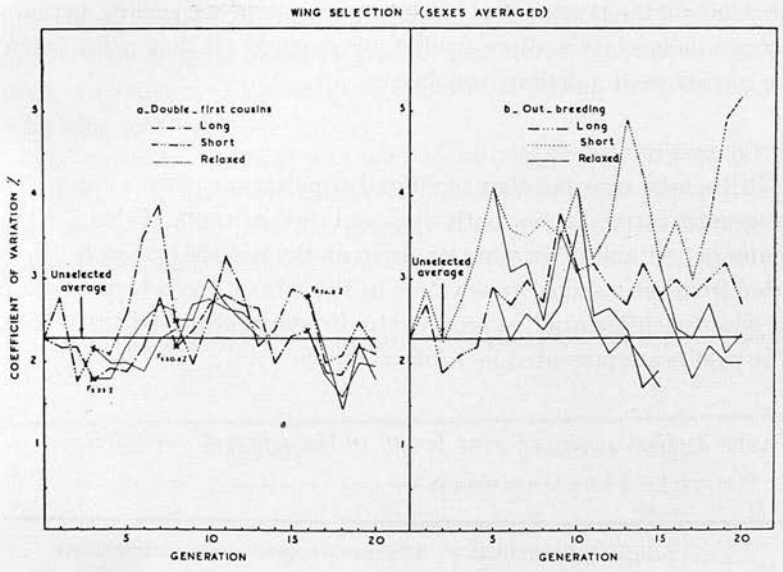

Fig. 4. Coefficient of variation for wing length in different selected lines of
a) Double–first cousins,
b) Outbreeding matings.

Coefficient of variation for wing length in lines carried out with matings between double–first cousins fluctuates above and below the control level in both the selected lines as shown in Figure 4*a*. The trends in the coefficients of variation in the outbred selected lines are of great interest, Figure 4*b*. They are higher than those of the unselected controls and they remain high from the earlier generations of selection. The line selected for short wing length shows higher coefficient of variation at almost every generation than that in the long wing selected line. The same results have been reported by ROBERTSON and REEVE (1952) and REEVE and ROBERTSON (1953). They explained the higher variance in the long wing line as due to selection being directed to the more heterozygous individuals to be the parents of the next generation. The higher variance in their short wing selected lines was due to segregation of one or both factors which appeared during

the course of selection, or increased variance was caused by high sensitivity of the wing curvature factor to environmental agency.

We may conclude that the high variance found in the selected outbred lines of the present study is due to more than one agency, perhaps actings in succession. More studies are required on that point before we can arrive at a definite conclusion.

3. *Changes in heritability*

It has been reported that the initial population carried a great deal of genetic variability for both wing and thorax length, Table 2. Estimates of heritability for wing length in all the selected lines were calculated from the response to selection as the ratio of the rate of advance to selection differential, as reported by ROBERTSON and REEVE (1952). The results are presented in Table 3*a* and *b*.

TABLE 3. *Heritability of wing length in the different selected lines*

a. Double-first cousins

Generation	Selection differential (1/100 mm)		Advance per generation (1/100 mm)		Heritability %	
	Long	Short	Long	Short	Long	Short
0– 5	2.68	—3.16	0.24	—1.66	8.9	52.50
5–10	2.75	—3.93	0.42	—3.24	15.3	82.40
10–15	6.33	—3.26	1.12	—0.52	17.7	15.90
15–20	5.59	—5.03	0.69	—0.43	12.3	8.60

b. Outbreeding

Generation	Selection differential (1/100 mm)		Advance per generation (1/100 mm)		Heritability %	
	Long	Short	Long	Short	Long	Short
0– 5	2.12	—4.81	0.16	—1.83	7.50	38.00
5–10	2.90	—3.75	—0.10	—1.51	—3.40	40.30
10–15	4.65	—4.57	—0.13	—2.24	—2.40	49.00
15–20	5.34	—5.15	0.73	—2.71	13.70	52.60

It can be seen from Table 3*a*, that the selected inbred line for long wing with double–first cousin matings shows a rapid decline in the heritability estimates from the first period of selection. The outbred line shows a rapid decline in the period of 5–15 as shown in Table 3*b*, followed by a rise to about 14% in the last period. Short wing selected lines show higher estimates in all systems of mating than that in the long wing selected lines.

The regression method was used to estimate more accurately the heritability of wing and thorax length in the various selected lines. The results secured from the progeny tests carried out in the case of the outbreeding system are tabulated in Table 4.

TABLE 4. *Heritability % of wing and thorax length in the outbred selected lines*

Generation	Wing length			Thorax length		
	Short	Long	D.F.	Long	Short	D.F.
5	43.4 ± 8	34.0 ± 2	18	47.2 ± 7	47.0 ± 6	18
10	59.8 ± 10	32.1 ± 5	18	36.1 ± 6	40.2 ± 6	18
15	45.4 ± 8	41.3 ± 6	16	42.1 ± 6	48.1 ± 8	16

Heritability of wing and thorax length estimated by the regression method clearly indicates that the selected outbred lines show a slight reduction.

Such a slight reduction appears in the long wing selected line, while the short wing selected line does not show any decrease in the heritability estimates.

These results clearly demonstrate that the outbred selected lines do not exhibit any marked decline in the genetic variance of body size from the initial foundation population. Throughout the experiment these lines appear to have a considerable high genetic variance for both wing and thorax length since they show a high phenotypic variance for these characters, and both size and variance decline as soon as selection is relaxed. The same results have been reported by REEVE and ROBERTSON (1953), who also observed that there was a real decline in the heritability estimates when selection was relaxed.

Changes of the genetic variability of wing and thorax length in the various selected inbred lines, in relation to different levels of inbreeding are presented in Tables 5 and 6 respectively. Heritability estimates are compared with each other between different systems of mating and with the theoretical expected decline as calculated by the equation given by LERNER (1950).

TABLE 5. *Heritability of wing length in the different selected inbred lines*

Coefficient of inbreeding %	Brother—sister				Double–first cousins			
	Long	Short	D.F.	Expected decline from 32%	Long	Short	D.F.	Exp. decline from 4
25	—	—	—	—	41.5 ± 5	48.6 ± 6	18	38.0
50	—	—	—	—	42.9 ± 4	40.2 ± 7	16	29.0
75	2.4 ± 10	14.0 ± 15	6	8.96 [1]	34.2 ± 5	32.6 ± 4	17	17.0

[1] $F_x = 78.52\%$.

TABLE 6. *Heritability of thorax length in the different selected inbred lines*

Coefficient of inbreeding %	Brother–sister				Double–first cousins			
	Long	Short	D.F.	Expected decline from 35%	Long	Short	D.F.	Exp. decline from 4
25	—	—	—	—	45.3 ± 6	46.6 ± 7	18	39.6
50	—	—	—	—	40.2 ± 6	46.3 ± 5	16	30.9
75	9.0 ± 14	7.0 ± 13	6	10.0 [1]	35.4 ± 7	37.6 ± 6	17	18.4

[1] $F_x = 78.52\%$.

It is clearly shown from Tables 5 and 6 that there is a reduction in all the estimates. The reduction is more distinct in lines maintained with brother–sister matings, where there is insignificant differences between the theoretical and observed values at the higher levels of inbreeding. Genetic variability estimated in the various inbred lines mated by double–first cousins indicates that there is a little change in the additive genetic variance at any given coefficient of inbreeding.

Heritability declines greatly in the case of matings between brothers and sisters, due to the increase of homozygosity within lines. This type of mating automatically tends to reduce heterozygosity, and by the time animals have reached the twentieth generation they are about 99% homozygous, and at this level the selected lines would show a much lower heritability estimate. Most of the variance at such a level of homozygosity is wholly due to the environmental effects. Thus we may conclude that the reduction expected from the known rate of inbreeding, particularly at the higher levels in case of sib matings, is not far beyond that actually observed.

These results indicate that selection with the more intensive inbreeding is more effective in decreasing the genetic variability than milder rates, which supports the view extended by TANTAWY (1952). The calculations of HAYMAN and MATHER (1953) and REEVE (1955) indicate that to attain homozygosity one should inbreed as rapidly as possible as well as minimize selection between lines.

4. *Genetic correlation*

Genetic correlation between wing and thorax length, which is the description of the relationship between the additive deviations caused by genes in the two traits, is found to be high in the initial foundation popuplation, Table 2.

In each progeny test carried out in the present study, genetic correlation was calculated by the application of the formulae given by REEVE (1953). The results for the different systems of mating are presented in Tables 7 and 8.

TABLE 7. *Genetic correlation between wing and thorax length in the selected outbred lines*

Generation	Genetic correlation %	
	Long	Short
5	106.0	100.0
10	80.0	78.0
15	76.0	83.0

Changes of the genetic variability of wing and thorax length in the various selected inbred lines, in relation to different levels of inbreeding are presented in Tables 5 and 6 respectively. Heritability estimates are compared with each other between different systems of mating and with the theoretical expected decline as calculated by the equation given by LERNER (1950).

TABLE 5. *Heritability of wing length in the different selected inbred lines*

Coefficient of inbreeding %	Brother—sister				Double–first cousins			
	Long	Short	D.F.	Expected decline from 32%	Long	Short	D.F.	Exp decli from 4
25	—	—	—	—	41.5 ± 5	48.6 ± 6	18	38.0
50	—	—	—	—	42.9 ± 4	40.2 ± 7	16	29.0
75	2.4 ± 10	14.0±15	6	8.96[1])	34.2 ± 5	32.6 ± 4	17	17.0

[1]) $F_x = 78.52\%$.

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Coefficient of inbreeding %	Brother–sister				Double–first cousins			
	Long	Short	D.F.	Expected decline from 35%	Long	Short	D.F.	Exp decli from 4
25	—	—	—	—	45.3 ± 6	46.6 ± 7	18	39.6
50	—	—	—	—	40.2 ± 6	46.3 ± 5	16	30.5
75	9.0 ± 14	7.0 ± 13	6	10.0[1])	35.4 ± 7	37.6 ± 6	17	18.4

[1]) $F_x = 78.52\%$.

It is clearly shown from Tables 5 and 6 that there is a reduction in all the estimates. The reduction is more distinct in lines maintained with brother–sister matings, where there is insignificant differences between the theoretical and observed values at the higher levels of inbreeding. Genetic variability estimated in the various inbred lines mated by double–first cousins indicates that there is a little change in the additive genetic variance at any given coefficient of inbreeding.

Heritability declines greatly in the case of matings between brothers and sisters, due to the increase of homozygosity within lines. This type of mating automatically tends to reduce heterozygosity, and by the time animals have reached the twentieth generation they are about 99% homozygous, and at this level the selected lines would show a much lower heritability estimate. Most of the variance at such a level of homozygosity is wholly due to the environmental effects. Thus we may conclude that the reduction expected from the known rate of inbreeding, particularly at the higher levels in case of sib matings, is not far beyond that actually observed.

These results indicate that selection with the more intensive inbreeding is more effective in decreasing the genetic variability than milder rates, which supports the view extended by TANTAWY (1952). The calculations of HAYMAN and MATHER (1953) and REEVE (1955) indicate that to attain homozygosity one should inbreed as rapidly as possible as well as minimize selection between lines.

4. *Genetic correlation*

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Generation	Genetic correlation %	
	Long	Short
5	106.0	100.0
10	80.0	78.0
15	76.0	83.0

TABLE 8. *Genetic correlation between wing and thorax length in relati to coefficient of inbreeding*

Coefficient of inbreeding %	Brother–sister [1]		Double–first cousins	
	Long	Short	Long	Short
25	—	—	88.0	92.0
50	—	—	78.0	82.0
75	40.0	19.0	73.0	66.0

[1]) $F_X = 78.52\%$.

Table 7, shows that the genetic correlation between wing and thora length remains quite high in the outbred selected lines with no chan in the later generations of selection. These results agree with tho reported by REEVE (1950), who found no differences in such geneti correlation of another stock of *Drosophila melanogaster* in lines selecte for long and short wing length. REEVE and ROBERTSON (1953) reporte a value of 75% for such genetic correlation in the unselected stoc increased to 86% in the long wing selected lines, and concluded tha continued selection tended to increase the genetic correlation. Result of the present study show that genetic correlation between wing an thorax length in the case of the outbred selected lines remains almos constant throughout the experiment.

Relating the changes that occurred in such genetic correlation wit the coefficient of inbreeding, Table 8, it can be noticed that there is tendency for it to decline in subsequent generations of brother–siste matings and remains, in general, stable in the case of double–first cou sins and only shows a slight reduction at higher levels of inbreeding.

Although this genetic correlation, in case of brother–sister, amounte to 40% and 19% in the long and short wing selected lines respectively at about 78% coefficient of inbreeding, they are probably not signifi cant.

5. *Effects on fertility*

During the course of the present experiments records have been kep for the number of eggs cultured in each vial and the number of adul flies hatched in each of the selected lines and in the control stock.

The percentage of eggs yielding flies are presented in Figure 5. It ca

be noticed from that figure that, in all the selected lines, fertility has declined below the control level from the early generations of selection. The control stock did not show any marked decline in its percentage emergence from the start point, showing throughout the experiment about 53%–56%.

As the result of increasing homozygosity, effects of inbreeding on percentage emergence are usually but not inveriably deleterious. In the present experiments the selected inbred lines show a decline in fertility below the control level, Figure 5, and in the case of brother–sister matings, TANTAWY (1956) showed that percentage emergence was more affected in the earlier generations of inbreeding.

Such results do suggest that genes responsible for differences in size also affect adversely the percentage emergence, or it may be linked to such genes, but if so the linkage must be quite high.

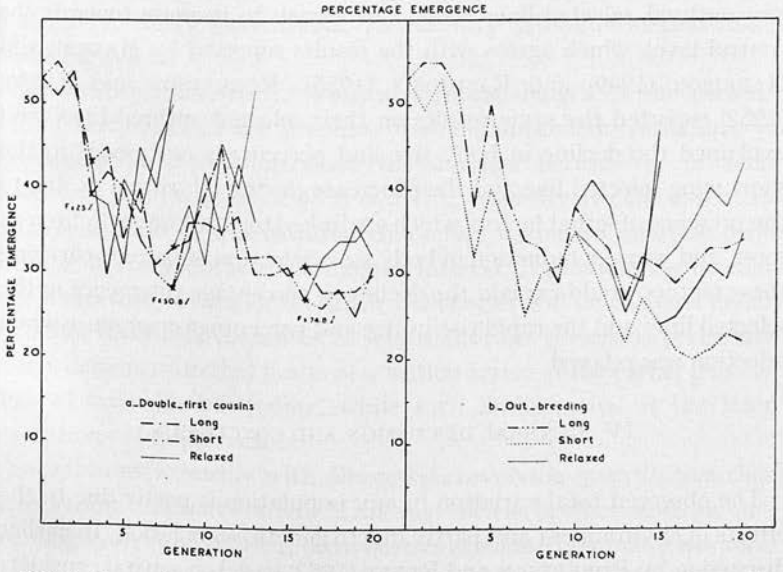

Fig. 5. Percentage of eggs yielding flies in the various selected lines of,
a) Brother–sister, and
b) Double–first cousin matings.

Results of percentage emergence after mass mating in the selected inbred lines with brother–sister matings may support the hypothesis of linkage between the two groups of genes. Body size and percentage

emergence remain almost constant after relaxing selection at high levels of inbreeding. It should be expected that fertility will increa in lines inbred with double–first cousin matings when selection wa relaxed at about 75% coefficient of inbreeding, since body size an phenotypic variation tended to return back by relaxation to the u selected level. This could be explained on the basis that selection wit inbreeding between cousins has fixed some of the genes which affec fertility adversely and have no effect on body size.

In the case of outbreeding matings, Figure 5*b*, the long wing selecte line shows higher percentage emergence than the same inbred line While the short wing outbred selected line behaves differently afte the tenth generation, it shows more reduction in fertility than the sam inbred lines. Throughout the experiment the long wing outbre selected line shows higher percentage emergence than that in the shor wing outbred line. With relaxed selection, fertility in both high an low outbred selected lines show, a tendency to increase towards th control level, which agrees with the results reported by MATHER an HARRISON (1949) and RASMUSON (1955). ROBERTSON and REEV (1952) reported the same results on their selected outbred lines, an explained the decline in body size and percentage emergence in th short wing selected line and their increase during relaxation as due t the presence of lethal factors which are linked together on each chromo some and cause a reduction in body size. Selection of parents carrying these factors would explain the decline in percentage emergence in th selected lines and the rapid rise in size and percentage emergence whe selection was relaxed.

IV. GENERAL DISCUSSION AND CONCLUSION

The observed total variation in any population is partly due to th effects of environment and partly due to genetic segregation. In earlie discussion by ROBERTSON and REEVE (1952) based on general consider ation, stressed that an allele substitution which affect a quantitativ character is likely to be greatly influenced by both genetic backgroun and environmental conditions. The relative importance of the two sort of variation give some indication of the effectiveness of selection, which is the only way to make a systematic change in the character concerned Thus, if most of the variation is due merely to environmental effects

superior individuals selected as parents are unlikely to transmit their superiority to their offspring. The part of the variation which is due to gene segregation is regarded as the effects of the additive genes togegether with variation due to dominance and to the effects of genes wich interact in an unpredictable manner. By calculating the correlation between various relatives it is possible to measure the average effects of genes which are transmitted from generation to generation. The fraction of the total variation observed in any population which is caused by differences between genes is called heritability. Estimation of such a fraction gives an indication of the extent to selection which is likely to be effective, i.e. the higher the heritability estimates the greater the prospect of successful selection provided disturbing factors do not intervene. Expected response to selection based on heritability analysis have not been always realized and an example of such situation was reported by REEVE and ROBERTSON (1953). They found that selection for increased wing length had reached a limit and the character unchanged for thirty generations. Heritability estimates at that time, was as high as 50%.

Heritability estimates of wing and thorax length of the present study clearly indicate the presence of abundant genetic variability in the fundation population since the average heritability of such characters was found to be 45% and 47% respectively. The extent to which variation of quantitative characters is due to additive gene effects is of considerable experimental interest. It provides the breeder with a measure of the rate at which a character will be changed under selection. Results of responses to selection of the present experiments clearly demonstrate that limits of selection arrive at the earlier generations of intensive inbreeding, while such limits arrive at the later generations of milder rates.

Selection experiments with *Drosophila* involving quantitative characters using different systems of mating, such as brother–sister or outbreeding systems of mating, have been investigated by many workers. The work of ZELLENY (1922). ZELLENY and MATTOON (1915) and MAY (1920) with brother–sister matings indicate that the response to selection declines or stops after a few generations of inbreeding, although PAYNE (1920) and RASMUSON (1949 and 1952) reported that selection is effective beyond the earlier generations. TANTAWY (1956), selecting for long and short wing length in *Drosophila melanogaster* with

brother–sister matings, found that selection in both the direction effective in increasing and decreasing wing length to the third gen ation, after which selected lines remained almost constant in si Response to selection in the short wing selected lines is much high than that found in the long wing selected lines. Selection for short wi length caused a decline of about 1.5% below the control level at 5 coefficient of inbreeding and then stabilized at this level.

Results of the present study indicate that response to selection i wing length shown by matings between double–first cousins is high than that in case of brother–sister matings. At the same, or nearly t same coefficients of inbreeding, brother–sister matings display less sponse to selection than that found in case of double–first cou matings, particularly in the small selected lines. Thus it could be co cluded that selection with milder rates of inbreeding is more effecti than with intensive one. Limits of selection in the latter mating be arrived at when the heritability of the selected character declines to significant values. ROBERTSON (1954) stated that, "Inbreeding redu size hence selection for small size is likely to create bias in favour homozygote combinations, especially those which particularly redu size. Unpublished experiments in which several different stocks we mass selected for small size, have demonstrated a steady response selection which ceased when the selected strains became apparent homozygous with respect to size, so there is good evidence that selecti for small size involves a progressive trend to homozygosity".

Selected lines maintained with outbreeding matings show great response in high and low directions than that found in the differe inbred selected lines. Response to selection in such selected lines more effective in the later generations, particularly after the tent At the twentieth generation the long wing selected line shows an i crease of about 3% over the control level and the short wing selecti line shows 19.5% below the control level. Limits of selection are n yet reached although these lines were carried out for twenty gener tions. These limits may be reached at a later stage of selection as fou by ROBERTSON and REEVE (1952). ROBERTSON (1952) and ROBERTS and REEVE (1953) stated that changes in long wing selected lines ha generally produced most effect in the third chromosome; while selecti for short wing in one strain tested produced effects mainly in t X-chromosome. They showed no evidence that selection for large a

small size had produced changes in the fourth chromosome, acting in the direction of selection.

In the present experiment, the short wing outbred selected line displays greater response to selection than that reported by ROBERTSON and REEVE (1952) on another stocks of *Drosophila melanogaster*, being compared at the same generations. Such different results in the re sponse to selection could be explained by the differences between the amount of the genetic variability initially available in the various foundation stocks.

It is pretty clear from the results secured from the present investigation that different inbreeding pressures lead, on the average, to fairly predictable results. One may conclude, therefore, from the response to selection in different systems of mating, that type of mating, i.e. the relationship between mated individuals, chosen by the breeder to maintain the various selected lines has a great effect on the response to selection.

Description of the response to selection for wing length brings us to the second general point, i.e. the power of correlated response to bring about changes in another character for which no direct selection is practised. Measurements of thorax length, in addition to wing length, were made during the course of the present study. Correlated response may be one of these two main types:

1. The characters are not correlated genetically. No response to selection would be expected in the secondary character, but it may show response to selection as the primary character for which selection was practised.

MATHER and HARRISON (1949) reported a case of such type in *Drosophila* and they attributed this behaviour to the break up of the balanced combination of linked genes.

2. The two characters are correlated genetically. The secondary character shows response to selection in the same direction as the primary character. ROBERTSON and REEVE (1952) and TANTAWY (1953 and 1956) reported this type of correlated response in *Drosophila*. They all found a high positive genetic correlation between wing and thorax length, and selection for wing length was accompanied with a change in thorax length in the same direction. But it seems that there is an exception to that rule. TANTAWY (1956) reported a case where genetic correlation between wing and thorax length in the Nettlebed

stock of *Drosophila melanogaster* was about 65% and found that selec tion for short wing in one of the selected lines was accompanied by lon thorax in spite of the high positive genetic correlation between them

These unexpected results were explained as due to linkage betwee genes affecting the two traits in different directions, or to the plei tropic effects of genes which decrease wing length and increase thora length.

In the initial foundation population of the present study ther existed an estimated genetic correlation between wing and thora length of about 82%. One may infer from such results that a change i wing length brought about by selection should be generally followe by a less than proportionate change in thorax length in the sam direction. This was found to be the case in all the different selecte lines; long and short wing selected lines show an increase and decreas respectively, in thorax length. Thus we may conclude that the genet correlation can be attributed more accurately as a basis for selectio of the two desirable traits than the phenotypic correlation betwee them since environment, dominance and epistasis greatly affect th latter correlation.

After mass mating in the case of brother–sister matings, TANTAW (1956) showed that relaxed selection has no effect on the variabilit of the selected lines as the coefficient of variation remained well belo the control level. These results indicate that the differences betwee high and low lines may be fixed after the 50% coefficient of inbreedin due to the increase of the homozygosity, thus agreeing fairly well wit those reported by ZELLENY (1922) and RASMUSON (1949 and 1952 Selection is also a factor that tends to decrease heterozygosity since th matings of only the largest and most vigorous pair of individuals pre sumably brings together gametes of like genetic constitution and thu increases the proportion of homozygotes in the progeny population Under the hypothesis of the increase of homozygosity, relaxed selectio does not after the variability of the inbred selected lines especially a higher rates of inbreeding. Unexpected results were reported by TAN TAWY (1956) in one of the lines selected for short wing length when coefficient of variation did not show the same stability after relaxe selection. The behaviour of this line was explained as due to the fac that selection for small size depended on selection of heterozygotes a

one or two loci, and that the fixation was prevented by low viability or the lethality of one of the alleles.

In general it is assumed that homozygosity increases with inbreeding and decreases variability. The results of brother–sister matings indicate clearly that that type of mating is accompanied by decrease in the phenotypic variability of wing and thorax length due probably to the decrease of genetic variability within lines. Phenotypic variation of both characters in lines maintained by double–first cousin matings fluctuates above and below the control level while it is much higher in the case of the outbred selected lines than in the unselected average. When selection was relaxed in both systems, phenotypic variation fell in subsequent generations to the control level. These results could be explained on the basis that selection in both systems was directed towards the more heterogenous individuals to be the parents of the next generation. The same results have been reported by ROBERTSON and REEVE (1952) and REEVE and ROBERTSON (1953) in their selected outbred lines.

Heritability of wing and thorax length, at the same coefficient of inbreeding, in the selected lines inbred with different rates, was estimated in order to test whether rate of inbreeding with selection influenced the amount of loss of heterozygosity for a quantitative character. Such estimates in the case of double–first cousin matings clearly indicate that there is little change in the additive genetic variance at any given coefficient of inbreeding; but it declines greatly in the case of brother–sister matings, especially at higher levels of inbreeding due to the increase of homozygosity within lines. On comparing the lines inbred at different rates, differences were found in the estimates of the heritability between selected inbred lines, i.e. brother–sister matings show heritability estimates almost to the expected decline at the higher levels of inbreeding while, at the same level, double–first cousin matings show slighter reduction. At about 78% coefficient of inbreeding, brother–sister matings show the values of 2.4% and 14%, and at about 75% coefficient of inbreeding double–first cousin matings show the values of 34% and 33% for long and short wing length respectively. Thus we may conclude from these results that the reduction of heritability estimates expected from known rate of inbreeding, especially in the case of brother–sister matings, is not far beyond that actually observed at higher levels of

inbreeding. These results indicate that the more intensive inbreedin with selection is more effective in decreasing genetic variability tha milder rates; probably this will be arrived at at the time selectio limits are achieved. Such results support the view observed by TAN TAWY (1952), who reported that intensive inbreeding with rando matings is more effective in eliminating heterozygosity at higher leve than milder rates.

Heritability estimates in lines maintained by outbreeding matin do not show any marked decline from the initial foundation populatio Throughout the present study these lines appear to have a conside able high genetic variance for both wing and thorax length, since the show a high phenotypic variance and both size and variance declin towards the control level as soon as selection was relaxed. It is foun that these lines maintain a high genetic variance for both wing an thorax length through the course of selection. Such results suppor those reported by REEVE and ROBERTSON (1953). Moreover, the reported that there was a real decline in the heritability estimate when selection was relaxed.

The general conclusion developed from the present study and tha reported by TANTAWY (1956) is that the cause of selection limits i different selected lines, particularly those inbred with brother–siste matings, is the loss of genetic variability. This conclusion rests primar ly on the basis that selection stabilizes at higher levels of inbreedin where heritability has declined greatly, almost to the theoretical expec tation. Selection is almost ineffective when all the favourable allele presented in the original population have been brought to fixatio and as the frequencies of such favourable alleles become greater, th genetic variance will declinc, as indicated by MATHER (1949). Thi fixation could be arrived at by selection with the more intensiv system of inbreeding through the increase of homozygosity within in bred lines. Selection with milder rates of inbreeding is based upo selection of the more heterozygotes individuals, since the heritabilit in the later generations of selection is high as much as in the initia population.

Animal breeders are familiar with the methods of calculating th coefficient of inbreeding and the loss of heterozygosity from pedigree Discrepancies found between the actual and expected rates of declin in genetic variance, from the present study and from that reported b

TANTAWY (1952) in the case of random matings, do suggest that no relationship exists between theoretical and actual homozygosity in random and selected lines. It may be expected, therefore, that the computed coefficient of inbreeding, particularly in milder rates of inbreeding, will overestimate the actual amount of homozygosity achieved, as indicated previously by MATHER (1950).

Genetic correlation between wing and thorax length is found to be high in the initial population, almost 82%. This genetic parameter remained, in general, stable at any level of inbreeding in the case of double–first cousin matings, while brother–sister matings, as reported by TANTAWY (1956), showed more reduction, particularly at the higher levels of inbreeding. At about 78% of inbreeding, such estimates were found to be 40% and 19% in case of brother–sister matings and at about 75% of inbreeding, these estimates are found to be 73% and 66% in the case of double–first cousin matings for long and short wing selected lines respectively. These estimates, in the former system, are probably not significant. As the genetic variability is reduced by inbreeding, we would expect that the genetic correlation declines also, and this was found to be the case in the selected inbred lines with sib matings.

In the case of outbreeding matings, such genetic correlation behaves differently than in the inbred selected lines; it remains almost constant. REEVE (1950) found no differences in the genetic correlation between wing and thorax length in long and short wing selected lines and the present results support REEVE's view in that respect. REEVE and ROBERTSON (1953) reported a value of 75% as the genetic correlation between the same traits in an unselected stock of *Drosophila*, and after selection this estimate was increased to 86% in the long wing selected line. They concluded that continued selection tended to increase such genetic correlation. The results thus presented show the stability of such genetic correlation in the outbred selected lines.

As the results of increasing homozygosity, effects of inbreeding on percentage emergence are usually, but not inveriably, deletorious. In the present experiments all the selected lines show a marked decline in percentage emergence below the control level. WIGAN and MATHER (1942) have shown that selection for high and low abdominal and sternopleural chaetae number in *Drosophila* usually result in a marked decline in productivity, even in inbred lines. The present results do

suggest that genes responsible for differences in size also affect adversely the percentage emergence or it may be linked to such genes. The stability of body size and percentage emergence after mass mating in the selected inbred lines with brother–sister matings, and the return of the two characters to the control level in case of double–first cousins, do support such an hypothesis.

The outbred selected lines show a decline in percentage emergence, the short wing selected line shows more reduction than the long wing selected line. The main response to selection for wing length is accompanied by a correlated response of decrease in fertility. These results agree fairly well with those reported by MATHER and HARRISON (1949), ROBERTSON and REEVE (1952) and RASMUSON (1955). When artificial selection is relaxed, fertility rises, as well as body size to the control level.

It should be concluded, therefore, that a close linkage between body size and fertility has been developed during selection with outbreeding mating system, through probably those genes affecting small size are linked with genes which affect fertility adversely.

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SUMMARY

1. The present experiments describe the effects of selection on wing length with two different systems of mating, i.e. doule–first cousin and outbreeding systems. A comparison has been made between the reuslts secured from such matings with those reported by TANTAWY (1956) in inbred selected lines with brother–sister matings. In each system of the present experiments, two parallel selected lines were maintained, one line selected for long wing and the other for short wing. Changes of wing lengths by selection, effects of relaxing selection, phenotypic variability, changes of heritability, genetic correlation between wing and thorax length, and viability have been studied in each of the selected lines and all of these results have been compared with the results of brother–sister matings.

2. Heritability estimates for wing and thorax length in the initial foundation population are found to be high; they are on the average about 45% for wing length and 47% for thorax length. The average genetic correlation between these two characters is found to be, on the average, 82%.

Selection in all systems of mating has been effective in increasing and decreasing wing length. Short wing selected lines display greater response to selection than long wing selected ones.

Long and short wing selected lines, with brother–sister matings, increase gradually from the first generation of selection to the third, and then stabilizes at this level. Inbred lines with double–first cousin matings yield more response to selection, being compared at the same coefficient of inbreeding, than in the case of brother–sister matings, and then stabilizes at about the thirteenth generation. Outbred selected lines show a gradual response to selection to the twentieth generation, i.e. to the end of the experiment. The outbred long wing selected line shows an increase of 3% over the control level and the short wing selected line shows a decrease of about 19.5% below the control level at the twentieth generation.

Thorax length shows almost the same response to selection in all the selected lines of the present experiments as in wing length, due to the high positive genetic correlation between them.

3. When selection was relaxed in the case of brother–sister matings at higher levels of inbreeding, i.e. 78%, relaxed selection has no effect on the selected character. In the case of double–first cousin and outbreeding systems of mating, selected lines returned back almost to the unselected level whenever selection was relaxed.

4. Coefficients of variation behave differently in the various systems of mating. In the case of brother–sister matings, this coefficient declines below the control level in both directions of selection to the third generation after which coefficient of variation remains almost constant. Relaxed selection has no effect, at higher levels of inbreeding, on the coefficient of variation.

In the case of double–first cousin matings, the coefficient of variation for wing length in both long and short selected lines fluctuates around the control level, while outbreeding matings cause an increase in this coefficient over the control level, particularly in lines selected

for short wing. When selection was relaxed, such selected inbred and outbred lines tend to return back to the control level.

5. Heritability of wing length, at higher levels of inbreeding, has declined in the selected inbred lines with brother–sister matings almost to the theoretical expectation. Heritability of such lines has declined to about 2.4% and to 14% in the long and short wing selected inbred lines, respectively, at about 78% coefficient of inbreeding.

In the case of double–first cousin matings, heritability has been reduced very slightly, i.e. insignificant reduction, at any given coefficient of inbreeding, while the outbred selected lines do not show any reduction in the heritability estimates at any given generation.

6. Genetic correlation between wing and thorax length is found to be quite high in the foundation population. This correlation has been decreased in the case of brother–sister matings, particularly at higher levels of inbreeding, to insignificant values. Matings between double-first cousins cause a slight reduction, while outbreeding matings show stability in such correlation.

7. Fertility has fallen in all the selected lines, there being more reduction in the outbred selected lines than in the inbred lines. When selection was relaxed, fertility remained almost constant in the selected inbred lines at higher coefficients of inbreeding, but it rises to the control level in the outbred selected lines whenever selection is relaxed. Double-first cousin matings show stability in fertility when selection is relaxed at higher levels of inbreeding, due, probably, to fixation of some genes affecting fertility adversely, and has no effect on body size.

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HETEROSIS AND GENETIC VARIANCE IN HYBRIDS BETWEEN INBRED LINES OF DROSOPHILA MELANOGASTER IN RELATION TO THE LEVEL OF HOMOZYGOSITY

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ALTHOUGH exploitation of heterosis in hybrid maize is so far the most successful single achievement of applied genetics, understanding of the causes responsible for this phenomenon remains still unsatisfactory. Much of the work on heterosis has been purely empirical and descriptive. Analytical studies have been conspicuously rare, and this in spite of the fact that heterosis is a term which, as most geneticists agree, is being applied to a group of "scarcely related phenomena" (DOBZHANSKY 1950). Only in recent years has interest in the investigation of the genetic bases of heterosis asserted itself. A symposium on heterosis was held in 1950 (edited by GOWEN 1952). CROW (1952), DOBZHANSKY (1952), HAGBERG (1953), MATHER (1955), RENDEL (1953) and others have discussed the different genetic mechanisms which may bring heterosis about.

Drosophila is the most important animal which has been used for experimental investigations of heterosis. Two main methods have been utilized. First, observations and experiments on the behavior of inverted sections of chromosomes in natural and laboratory populations have been described by DOBZHANSKY and his colleagues. Secondly, lines inbred by different methods are crossed, and different morphological and physiological characteristics of the hybrids and the inbreds measured and compared (ROBERTSON and REEVE 1952, 1954, 1955a, b; RASMUSON 1952; CLARKE and MAYNARD SMITH 1955; TANTAWY 1955 and others). The results obtained are variable for different traits and different situations. In order to understand these variations, careful analysis of the genetic systems by which the inbreeding has been brought about is indispensable.

The experiments reported in the present communication have been designed to study the relationships between the rates of inbreeding and the observed inbreeding degeneration and restoration of heterosis by crossing. The relation between the genetic variances observed in the inbred lines and in the hybrids between them has also been studied.

MATERIALS AND TECHNIQUES

The stock used in the present experiments is the Crianlarich stock of *Drosophila melanogaster*, which has been kept in the laboratory in populations of 20 pairs of flies per bottle. The same stock has been used by TANTAWY (1956b, 1957) and by ROBERTSON and REEVE (1955a, b).

In the present study two systems of mating have been used, starting with the initial foundation population. These systems are (a) Brother-sister, and (b) Double-first cousin matings. The details of these systems of mating have been explained elsewhere

by TANTAWY (1956b). In each system of mating five parallel lines have been maintained. The general procedure in maintaining these lines and the heritability estimates for wing and thorax length in the foundation population as well as in the different inbred lines have been given by TANTAWY (1957).

At approximately the same theoretically computed levels of homozygosity, i.e. at 25 percent, 50 percent and 75 percent inbreeding coefficients, the five parallel inbred lines within each system of mating were intercrossed; the hybrids were examined for indications of heterosis, using as criteria wing and thorax length and also percentage emergence of adults from a given number of eggs. From each cross five pair matings were made, allowed to mature for three days, and then transferred to oviposition vials for collection of eggs. Eggs were cultured in vials (not more than 70 eggs in each vial) containing the usual cornmeal-molasses-agar medium fortified with additional dried baker's yeast and well yeasted with live yeast. The eggs were collected and cultured from each pair mating, on four successive days. The number of eggs cultured, and of adults hatched in each culture, were recorded to estimate the percentage emergence. Wing and thorax length were measured on ten pairs of progeny (ten males and ten females), from each of the 50 pair matings in each system and from each culture on the first two days.

At 25 percent, 50 percent and 75 percent coefficients of inbreeding, in each system of mating, progeny tests have been carried out to estimate the heritability of body size in the F_2 from crosses between the inbred lines. At the known rate of inbreeding within each system of mating, ten such F_2 families have been established, one family from each cross. In each F_2 five males and five virgin females were measured, and four pairs were mated assortatively, i.e. first largest male to first largest female, second largest male to second largest female, and first smallest male to first smallest female, second smallest male to second smallest female. These forty pair matings from the ten families were fed for three days and then transferred to oviposition vials for collection of eggs which were introduced into cultures on four successive days. After emergence five females were measured on each of the first two days, which gives 40 females in each progeny test.

Genetic parameters of the initial population

Two progeny tests have been carried out in the initial foundation stock. The heritability of wing and thorax lengths and the genetic correlation between them as reported by TANTAWY (1957). The weighted means of the heritability estimates derived from the various progeny tests are 38.51 ± 4.30 percent and 37.77 ± 4.1 percent for wing and thorax length respectively, with an average genetic correlation of 0.74 between them.

Heritability estimates in inbred lines and in hybrids

Heritability estimates for wing and thorax length with the two systems of mating derived from the regression of offspring size of mid-parent size, are presented in table 1 for wing and for thorax length. As the female progeny only were measured, the heritability estimates were corrected, at the levels of homozygosity studied, for the

TABLE 1

Heritability in inbred lines and crosses at different levels of inbreeding

Mating System	F_x	Theoretical* h^2	Inbred Lines			Hybrids	
			Observed h^2	N	Ratio Observed Theoretical	h^2	N
Wing Length							
Brother-sister	25.0	31.95	43.98 ± 7.48	40	1.4	27.36 ± 8.18	38
	50.0	23.84	37.54 ± 6.48	37	1.6	51.42 ± 4.57	36
	73.4	14.26	15.13 ± 8.83	37	1.1	48.10 ± 6.70	37
Double-first cousin	25.0	31.95	39.40 ± 5.65	40	1.2	49.29 ± 5.09	40
	50.8	23.70	34.04 ± 7.93	37	1.4	28.12 ± 7.14	38
	74.8	13.62	29.47 ± 3.52	39	2.1	26.14 ± 4.37	40
Control	0		38.56 ± 4.30	144			
Thorax Length							
Brother-sister	25.0	31.28	27.76 ± 6.33	40	0.9	53.61 ± 9.02	38
	50.0	23.28	21.70 ± 7.15	37	0.9	47.19 ± 10.67	36
	73.4	13.88	14.79 ± 8.41	37	1.1	59.14 ± 10.04	37
Double-first cousin	25.0	31.28	44.03 ± 10.48	40	1.4	41.86 ± 6.63	40
	50.8	22.99	37.89 ± 11.67	37	1.6	26.27 ± 8.30	38
	74.8	13.25	28.92 ± 7.61	39	2.3	32.81 ± 8.30	40
Control	0		37.77 ± 4.20	144			

* Derived from F_2 from crosses between inbred lines.

absence of male measurements with the aid of the equation given by TANTAWY 1957). In each case the theoretically expected decline of the heritability estimates from the starting point is computed with the aid of WRIGHT'S equation (1921).

At the lower level of inbreeding the heritability estimates for wing and thorax length do not differ significantly from the value found in the parent population. At 75 percent coefficient of inbreeding, lines inbred by brother-sister mating show a definite decline and the observed heritability agrees well with the theoretically computed value. With a milder rate of inbreeding, however, the decline is much less, presumably due to the action of natural selection in slowing down the rate of approach to homozygosis. The contrast is clearly seen in the ratio of observed to theoretical heritability at the different levels in inbreeding. These results are in agreement with those reported by TANTAWY and REEVE (1956) in a similar study based on four different mating systems and by TANTAWY (1956a, b).

When the inbred lines are crossed within each system of mating, the heritability estimates derived from the F_2 generally exceed the values found in the parent lines and are about the same as the estimate derived from the parent population.

TABLE 2

Wing and thorax length (in microns) for inbred lines and hybrids between them at different coefficie inbreeding (F_x)

Wings

Mating system	F_x	Inbreds		Hybrids		Heterosis (percentage
		Size	N	Size	N	
Brother-sister	Controls	1901.23 ± 7.04	80	1901.23 ± 7.04	80	–
	25.00	1890.02 ± 2.07	200	1895.00 ± 1.21	964	0.27 ± 0.
	50.00	1849.14 ± 3.18	191	1868.30 ± 2.48	1000	1.04 ± 0.
	73.44	1831.54 ± 2.48	195	1877.50 ± 6.27	908	2.51 ± 0.
Double-cousins	25.00	1892.37 ± 2.54	200	1899.70 ± 3.78	1000	0.39 ± 0.
	50.78	1898.36 ± 2.69	200	1910.21 ± 5.03	1000	0.63 ± 0.
	74.82	1895.64 ± 2.93	200	1911.29 ± 4.18	1000	0.83 ± 0.

Thorax

Brother-sister	Controls	967.60 ± 8.29	80	967.60 ± 8.29	80	–
	25.00	955.61 ± 1.03	200	952.07 ± 1.72	964	−0.37 ± 0.
	50.00	951.20 ± 2.33	191	955.72 ± 2.36	1000	0.48 ± 0.
	73.44	939.32 ± 4.96	195	956.88 ± 4.66	908	1.87 ± 0.
Double-cousins	25.00	966.05 ± 1.20	200	959.77 ± 3.27	1000	−0.65 ± 0.
	50.78	979.63 ± 1.33	200	983.67 ± 2.03	1000	0.41 ± 0.
	74.82	963.78 ± 1.57	200	974.74 ± 1.94	1000	1.14 ± 0.

N = Number of flies measured.
† = Significant at the level of 2 percent.
* = Significant at the level of 5 percent.

Heterosis in wing and thorax length

Table 2 shows that the reduction of average size, measured as either wing or th length, follows essentially the same pattern as that revealed in the study of her bility. Lines inbred by brother-sister mating, show significant decrease in size higher levels of inbreeding, while, with cousin mating, the decrease is very slight e at the highest theoretical level. TANTAWY and REEVE (1956) noted a similar tende for body size to decline only at higher levels of inbreeding.

When the inbred lines within each system of mating are intercrossed, the generally exceeds the mid-parent level (table 3). The percentage heterosis i.e. rati average F_1 to average parent size, tends to be greater in the brother-sister than double-first cousin series, especially at 75 percent level of inbreeding. Evidently magnitude of this heterosis is closely related to the extent to which the parent li have declined below the level of the outbred stock.

Phenotypic variation

Table 3 shows the phenotypic variation in the inbred lines and crosses in term coefficient of variation. In wing length, inbreeding leads to a decline in the coeffi

TABLE 3

Coefficients of variation for wing and thorax length in inbred lines and hybrids between them at different coefficients of inbreeding (F_x)

Item	Brother-sister			Double-first cousins		
	F_x	Inbreds	Hybrids	F_x	Inbreds	Hybrids
Wing	Controls	2.42 ± 0.07	2.42 ± 0.07	Controls	2.42 ± 0.07	2.42 ± 0.07
	25.00	2.57 ± 0.10	2.00 ± 0.05	25.00	2.40 ± 0.04	2.05 ± 0.04
	50.00	1.95 ± 0.11	1.76 ± 0.03	50.78	1.92 ± 0.10	1.82 ± 0.03
	73.44	1.54 ± 0.06	1.23 ± 0.03	74.82	1.92 ± 0.08	1.70 ± 0.02
Thorax	Controls	2.76 ± 0.10	2.76 ± 0.10	Controls	2.76 ± 0.10	2.76 ± 0.10
	25.00	3.58 ± 0.10	2.73 ± 0.08	25.00	3.28 ± 0.08	2.68 ± 0.13
	50.00	2.26 ± 0.11	2.27 ± 0.04	50.78	2.48 ± 0.09	2.28 ± 0.06
	73.44	2.24 ± 0.07	2.20 ± 0.03	74.82	2.85 ± 0.09	2.13 ± 0.06

of variation from about 2.4 in the foundation stock, to 1.54 and 1.92 in the brother-sister and double-first cousin series at the theoretical level of 75 percent and this is reasonably consistent with the progeny test data. But, in the case of thorax length, the decline is relatively less for both mating systems and, in the milder system of inbreeding, there is really no evidence of any decline of variability. There is no obvious explanation for this discrepancy between the two dimensions. It may be related to the tendency for inbreeding to increase the relative importance of environmental variation (ROBERTSON and REEVE 1955b); there is probably evidence of this effect in the regularity with which the F_1 hybrids are less variable than their parents. But we might expect wing and thorax length to behave in much the same way with respect to variability in different genetic situations.

Percentage emergence

Percentage emergence is calculated from the ratio of the number of flies hatching from cultures to the number of eggs set up. The results are presented in table 4. Since the general level of percentage emergence fluctuates from experiment to experiment, records were obtained from the control stock in each of the tests carried out at different times. The inbreds are clearly less viable than the controls. Significant decreases in the percentage emergence are particularly clear at the higher levels of homozygosity.

TABLE 4

Percentage emergence in inbred lines and hybrids between them at different coefficients of inbreeding (F_x)

Mating system	F_x	Controls	Inbreds	Hybrids	Heterosis (percent)
Brother-sister	25.00	60.89 ± 3.05	59.94 ± 2.33	58.76 ± 2.64	−1.97 ± 0.61
	50.00	56.07 ± 3.92	48.89 ± 4.95	56.01 ± 1.01	14.56 ± 2.30
	73.44	61.55 ± 3.52	46.71 ± 1.08	57.76 ± 2.53	23.65 ± 4.50
Double-cousins	25.00	—	—	—	—
	50.78	53.58 ± 5.15	52.19 ± 1.46	52.17 ± 2.50	−0.03 ± 0.10
	74.82	65.71 ± 2.11	52.48 ± 2.98	58.60 ± 3.03	11.66 ± 2.11

Also, at any given coefficient of inbreeding, the inbred lines maintained by broth sister mating are less viable than those maintained by double-first cousin mat This confirms the results reported by TANTAWY (1957) and TANTAWY and RE (1956) for random inbred lines, and by TANTAWY (1956a, b) for selected inbred li

When the inbred lines are crossed, the F_1 progeny of the sib matings show a gre heterosis than the lines with milder rates of inbreeding. The hybrids show about same percentage emergence as the controls. Again we find a positive correla between the extent of inbreeding depression and the magnitude of heterosis.

DISCUSSION

Although inbreeding is one of the useful tools in the practical work of animal i provement, its results are often harmful. This contradictory situation has be epitomized by DARWIN (1876) in his famous phrase: "Although free crossing is danger on the one side which everybody can see, too close inbreeding is a hidd danger on the other". A multiplicity of causes which bring heterosis about is probab responsible for this apparently erratic behavior of inbred and outbred strains.

It has been recognized for many years that inbreeding increases the numbe homozygous loci, and therefore undesirable recessives become manifested which, w outbreeding, would be hidden in heterozygotes by their dominant alleles. Since m mutations are harmful, and since deleterious dominants are eliminated by natu selection more rapidly than deleterious recessives, normally outbred populations always carry unfavorable recessive mutant genes in a concealed condition. T mechanism has been called mutational heterosis by DOBZHANSKY (1952). On the oth hand, different alleles in an outbred Mendelian population may be mutually adjus or coadapted by natural selection, to produce favorable heterozygotes. Heterosis then, a consequence of overdominance rather than of simple dominance. This is balanced heterosis of DOBZHANSKY (1952), of MATHER (1955), and of LERNER (19 Finally, the possession of the greater variety of alleles at many gene loci may con upon the organism a superior adaptedness because of a greater biochemical versati as suggested by ROBERTSON and REEVE (1952), LERNER (1954), HALDANE (19 MAYNARD SMITH *et al.* (1955) and others. This effect could be observed both wit populations and in hybrids between populations which do not hybridize in nature

Body size and percentage emergence of adults from a given number of eggs are different "characters", in the sense that they can be studied separately in quantitat terms. In the experiments reported in the present paper, both characters decline inbred lines compared to the foundation stock. When the inbred lines are intercross the F_1 hybrids generally fall within the range of variation of the foundation popu tion. Body size declines however relatively less than does the percentage emerge This agrees with the observations of ROBERTSON and REEVE (1955b) that the bo weight in inbred lines declined by anything between 0 and 30 percent, while production was usually reduced by more than 50 percent when newly establis stocks are inbred.

More significant for our purposes is the observation that the extent of the breeding depression depends upon the closeness of the relationship between mated individuals in the inbred lines. Indeed, the lines inbred by brother-sis

matings have shown greater decline in thorax length, wing length and percentage emergence than did the lines inbred by double-first cousin matings. Conversely, when the inbred lines are intercrossed, the lines inbred by more intensive method show a greater percentage of heterosis than do the lines inbred by cousin matings. The magnitude of heterosis is, therefore, proportional to the degree of the inbreeding degeneration. With brother-sister and with cousin matings, average size and percentage emergence in the hybrids between the inbred lines is equal to that observed in the foundation population.

These facts are compatible with the hypothesis that the heterosis is, in this case, due mainly to the adaptive norm in the foundation stock consisting chiefly of heterozygotes for gene alleles or gene complexes in one or more chromosomes. This balanced heterosis is disturbed by the inbreeding, but the increase in frequency of homozygosis induced by inbreeding will be at least partially counteracted by natural selection in the experimental cultures. It appears that an equivalent level of homozygosity, especially higher levels, requires many more generations with milder forms of inbreeding, such as double-first cousin mating, than with brother-sister mating. The opportunity for natural selection to counteract the homozygosis induced by inbreeding will, then, be greater with cousin matings than with matings between sibs. In other words, coefficients of inbreeding theoretically computed will, in reality, correspond to a greater degree of homozygosis with sib matings than with cousin matings. When the genetic system involves heterozygote superiority, for one reason or another, natural selection and inbreeding will be more drastically affected than when heterosis is of the mutational type. This view is further supported by the fact that the observed heritability is consistently higher than expected with the less drastic form of inbreeding. This is evidently a form of "genetic homeostasis" postulated by LERNER (1954).

Another observation of interest concerns the changes in the phenotypic variance of wing and thorax length (table 4). Among 12 possible comparisons, 11 give either significantly or at least ostensibly lower variation coefficients in the F_1 hybrids than in the parent inbred lines. There is less consistency in comparisons between the inbred lines and the foundation stock, except that at higher levels of inbreeding the variability tends to decrease, at least with brother-sister matings. But the variability among hybrids is consistently below that in the controls. These relations are understandable if inbreeding decreases the genetic variance, while homozygosis increases and heterozygosis decreases the environmental variance. Indeed, ROBERTSON and REEVE (1952, 1955a, b), REEVE and ROBERTSON (1953) and RASMUSON (1952) observed reduction of the variability with increasing levels of heterozygosity and vice versa, and suggested this was associated with a greater biochemical versatility of heterozygotes. DOBZHANSKY and WALLACE (1953), DOBZHANSKY, PAVLOVSKY and SPASSKY (1955) and DOBZHANSKY and LEVENE (1955) observed the same phenomenon in homozygotes and heterozygotes for chromosomes found in natural populations of several species in Drosophila. They concluded that heterozygotes, in populations having the genetic structure like those of Drosophila, possess superior homeostatic adjustments to those in the homozygotes. This is especially striking with rare homozygotes which are "supervital", i.e. possess a higher viability than the average heterozy-

gote in certain environments. Yet these "supervital" homozygotes become subvi when the environment is changed. Heterosis, then, is expressed in an improvem and inbreeding degeneration in a decline, of homeostatic adjustments to envir mental changes. How far this rule holds for organisms other than Drosophila i matter for future studies.

SUMMARY

1. A number of parallel inbred lines of *Drosophila melanogaster* were maintained using two systems of mating, i.e. brother-sister and double-first cousin matings.

2. The heterosis for wing and thorax length and for percentage emergence w studied by crossing the various inbred lines within each system of mating at the sa or nearly the same coefficients of inbreeding.

3. Regression of offspring size on mid-parent size for the initial foundation popul tion gives heritability estimates for wing and thorax length of 38.51 ± 4.30 perce and 37.77 ± 4.80 percent respectively. Estimates at about 25 percent, 50 perce and 75 percent coefficients of inbreeding indicate no decline in heritability in lin inbred by double-first cousin matings. In brother-sister matings the heritability do not decline appreciably up to about 50 percent inbreeding but at 75 percent inbree ing, the values for both wing and thorax length are close to those th oretically expected.

4. In the hybrids between the inbred lines, heritability rises to about the val observed in the foundation population.

5. Percentage emergence is decreased more in lines inbred by brother-sister matin than in those inbred by mating of double-first cousins, especially at higher levels inbreeding.

6. Heterosis in crosses between lines was recorded for wing and thorax length a also for percentage emergence. This heterosis is significant in the hybrids betwe lines inbred by brother-sister matings to 50 percent and 75 percent of inbreeding, b in crosses between the lines inbred by cousin mating significant heterosis is observ only at 75 percent of inbreeding. At similar levels of inbreeding the lines inbred b brother-sister matings display a greater heterosis than those inbred by matin between cousins.

7. Phenotypic variation, as measured by coefficients of variation, decreases mo rapidly in the earlier generations of inbreeding. The lines inbred by brother-sist matings are less variable than those inbred by cousin matings. Phenotypic variati in the F_1 progenies is less than that of the parental lines.

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SELECTION LIMITS WITH SIBMATINGS IN DROSOPHILA MELANOGASTER

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EXPERIMENTS with Drosophila have been undertaken by many investigators to study the effects of selection on different quantitative characters. In such experiments, the parents of the next generation are always selected because they show a deviation in the direction desired from their population mean. A survey of the earlier investigations has been given by TANTAWY (1956a, b) using wing length in *Drosophila melanogaster* as the selection criterion. Other analyses of selection phenomena have been published by CLAYTON *et al.* (1957a b c), FALCONER and A. ROBERTSON (1956), PREVOSTI (1956), RASMUSON (1956), SCOSSIROLI (1956), and MARIEN (1958). They all agree that selection is effective in plus and minus directions; the latter showing greatest deviations from the initial population. The results demonstrate that the response to selection is limited; sooner or later selection limits are reached beyond which the character cannot be altered. It has been also shown that back selection and relaxed selection in negative and positive directions may result in rapid return to the control level in some experiments (TANTAWY 1956) and ROBERTSON and REEVE (1952) but not in others (TANTAWY 1956a). Recently, LERNER (1958) discusses the quantitative aspects of selection and presented the subject in a very lucid and full manner.

The present experiments were designed to provide information as to how long the response to selection may continue in highly inbred lines of *Drosophila melanogaster*.

MATERIALS AND TECHNIQUES

The stock used for the present experiments was the Carianlarich stock which has been kept by mass mating of 20 pairs of flies per bottle in every generation.

Technical procedures followed in the present experiments for control of environmental variations, matings between selected parents, method of selection and estimation of the heritability of body size, were similar to those reported previously by the author (1956a, 1957a). Experiment I with lines A and C, and experiment II with lines B and D were carried out during the years 1955 and 1956, respectively. In both experiments, lines A,B and C,D were maintained by selection for long and short wing length. In all the lines, matings between brothers and sisters were made. A control stock had been kept by mass mating for each experiment under environmental conditions similar to those of the selected lines.

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Selection in both experiments was relaxed at the first, seventh, tenth and twentieth generations, at which times coefficients of inbreeding should have been about 25, 78, 88 and 99 percent, respectively, for five successive generations. Heritability of the body size was estimated first for the initial foundation population, and then at the different levels of homozygosity indicated above.

RESULTS

Heritability of wing and thorax length in the initial foundation population

Heritability of body size *i.e.*, wing and thorax length, in the initial foundation population was estimated by the method of the regression of offspring on mid-parent as reported by TANTAWY (1957a). Six progeny tests were carried out, three of which involved random matings and three involved assortative matings, the latter being corrected for the magnified variance between the parents as indicated by REEVE (1953).

TABLE 1

Heritability of wing and thorax length, with their respective standard errors, and the genetic correlation between them in the initial foundation population

Progeny test no.	Mating system	Heritability percent		No. of matings	Genetic correlation percent
		Wing length	Thorax length		
1st (Oct. 1954)	Random	41.25±4.50	46.50±5.20	100	84
2nd (Feb. 1955)	Random	47.32±4.05	48.21±3.12	100	78
3rd (Oct. 1955)	Random	43.52±3.21	45.05±3.52	100	81
4th (July 1955)	Assortative	45.00±6.06	47.12±6.05	100	83
5th (Feb. 1956)	Assortative	41.12±5.30	42.06±4.51	97	80
6th (July 1956)	Assortative	41.01±6.57	43.00±5.01	98	79

The results obtained from the various progeny tests and the respective standard errors are presented in Table 1, where the data for each progeny test are given. The weighted means for all tests show that 43 and 45 percent of the total variance for wing and thorax length, respectively, are apparently due to the additive genetic variance. After correction for the magnified variance between the parents in the assortative test, the average genetic correlation was found to be 80 percent.

These results agree fairly well with those reported by REEVE and ROBERTSON (1953), TANTAWY (1957a, b) and TANTAWY and REEVE (1956) who showed that the additive genetic variance for wing length in *Drosophila melanogaster* ranged between 30 percent and 45 percent.

Selection responses in wing and thorax length

Selection responses in all selected lines were measured as their deviations from the control stock of a mass mated population reared under similar environmental conditions as the experimental lines.

TANTAWY (1956b) has shown the absolute size of the Carianlarich population of *Drosophila melanogaster* which has been used in the present study. The results obtained with both sexes were averaged since no differences between sexes have been observed. The main features of the response to selection for wing length are presented in Figure 1.

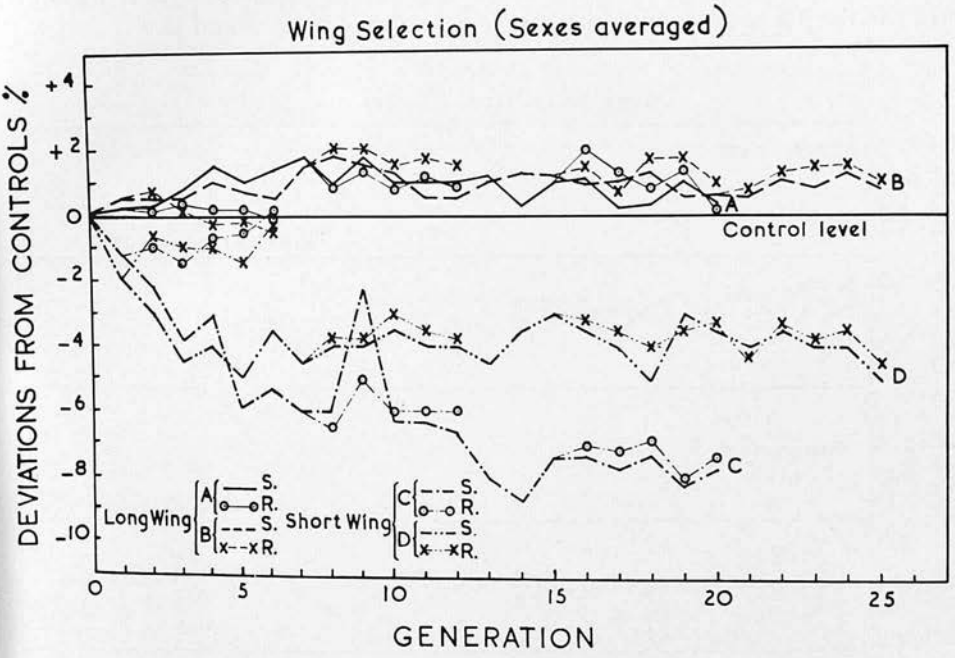

FIGURE 1.—Percentage deviations of wing length from controls, sexes averaged, where A,B,C,D, are the selected lines and S=selected and R=relaxed.

Examination of Figure 1 shows that selection is effective in both plus and minus directions, but that selection for small size shows greater response than that for large size. Figure 1 also demonstrates that lines A and B, selected for long wing, followed almost the same general trend. In both lines selection was effective to the fourth generation; they showed 1.5 and 1.0 percent deviations from the control level, respectively; the lines then remained almost constant throughout the experiments.

Lines C and D selected for short wings behaved in a different manner. Both lines responded similarly to selection for the first five generations and then diverged with line C (shown in Figure 1) producing a greater response. Selection was effective in both lines to the fifth generation, after which there was a tendency for them to remain stable to the end of the experiments. Such differences in the response to selection after the fifth generation between lines C and D could be attributed to some environmental factors which affect the selected and the control lines differently.

Similar results were achieved also for thorax length (results not included) this is to be expected because of the high positive genetic correlation betwee wing and thorax measurements (Table 1).

Phenotypic variance

Phenotypic variation for wing length is expressed as coefficients of variati and the results are presented in Figure 2 for experiments I and II.

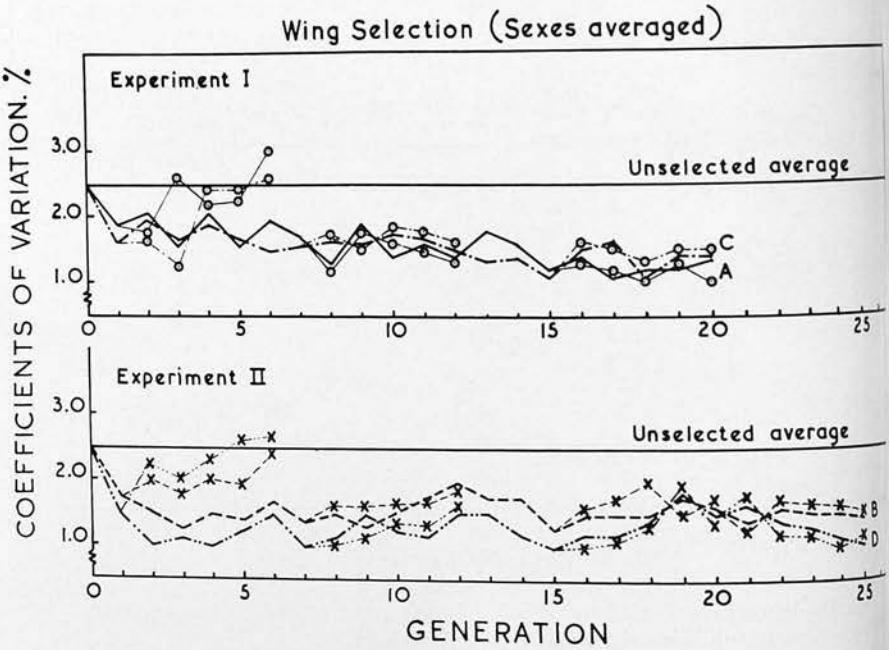

FIGURE 2.—Coefficients of variation for wing length (sexes averaged) in the different sele lines. For symbols see Figure 1.

It is clear that intensive inbreeding in both experiments caused a reductio the phenotypic variation of the selected inbred lines. Lines selected for short w length are less variable than those selected for long wing. In all the lines, phe typic variation declines in the earlier generations of inbreeding and then st lizes. Thorax length behaves similarly as wing length (unpublished materi

Relaxed selection

The effects of relaxed selection on wing length, as shown in Figure 1 at differ coefficients of inbreeding, indicate that relaxed selection at 25 percent coeffici of inbreeding causes an increase in the phenotypic variance to the control le in all the selected lines. At higher levels of inbreeding, relaxed selection has effect whatsoever on the response, *i.e.* relaxed selected lines remain almost co stant.

Heritability estimates in the selected lines

The heritability of wing length can be estimated as the ratio of rate of advance per generation to selection differential, the latter being the average deviation of parents from the mean size of their generation (ROBERTSON and REEVE 1952; TANTAWY 1956a). The results are presented in Table 2.

TABLE 2

Heritability of wing length in the selected lines

a. Lines A and C.

Generation	Selection differential		Advanced per generation		Heritability percent	
	Long A	Short C	Long A	Short C	Long A	Short C
0–5	3.18	—2.83	0.85	—1.71	26.7	60.4
6–10	3.18	—3.23	—0.10	—1.08	—3.1	33.4
11–15	3.73	—3.99	—0.20	—1.61	—5.4	40.4
16–20	2.75	—1.99	—0.30	—0.04	—1.1	2.0

b. Lines B and D.

	Long B	Short D	Long B	Short D	Long B	Short D
0–5	3.15	—2.95	0.78	—1.65	24.7	55.9
6–10	2.80	—3.06	0.02	—1.00	0.7	32.6
11–15	3.05	—2.85	—0.25	—1.53	—8.2	53.7
16–20	2.50	—3.05	—0.05	—0.25	—2.00	8.2
21–25	2.21	—2.75	0.11	—0.21	4.9	7.6

Table 2 shows that the heritability of wing length in the long wing selected lines declined after the first five generations to insignificant values, while in short wing selected lines heritability estimates for wing length showed higher values up to the fifteenth generation.

The regression method was used to estimate more accurately the heritability of wing length in the various selected lines, at different levels of homozygosity. The results secured from such analyses are presented in Table 3. It will be noticed

TABLE 3

Heritability of wing length, by the regression method, in the selected lines at different levels of inbreeding

Generation	Coefficients of inbreeding percent	Experiment I				Experiment II			
		Long		Short		Long		Short	
		h^2	D.F.	h^2	D.F.	h^2	D.F.	h^2	D.F.
1	25.00	38.5±5	18	42.3±4	18	35.2±4	18	40.5±3	18
5	67.2	19.4±6	18	23.2±7	18	17.2±4	18	25.3±5	18
10	88.6	6.2±4	18	10.3±6	18	5.3±2	18	10.2±3	18
15	96.1	4.3±4	16	7.6±4	18	4.2±3	14	8.3±2	16
20	98.6	3.2±2	16	5.6±3	16	6.2±4	16	5.3±4	16
25	99.5	....	..	....	..	3.1±2	14	4.3±3	16

in Table 3 that heritability of wing length declined in all lines after the fir generation of inbreeding, i.e., after 67.2 percent coefficient of inbreeding.

The most interesting feature of the results as presented in Table 2 and 3 is th contrast in the estimates of heritability, particularly in the short wing selec lines, according to whether heritability is computed from the ratio of adva per generation to selection differential or from the regression of offspring on m parent size. The higher values in Table 2 reflect the decline in size due to inbre ing which is confounded with the effects of selection. The long wing selected li show better agreement between the alternative estimates.

Effects of relaxed selection on the heritability estimates of wing length a shown in Table 4. The data in Table 4 indicate that the heritability decli

TABLE 4

Heritability of wing in the selected lines before and after relaxation at different levels of inbreeding

Coefficients of inbreeding	Before relaxation				After relaxation			
	Experiment I		Experiment II		Experiment I		Experiment II	
	Long	Short	Long	Short	Long	Short	Long	Short
25.0*	38.5±5	42.3±4	35.2±4	40.5±3	40.2±5	44.2±3	45.2±3	50.2±
78.5*	12.8±3	18.3±6	10.2±3	32.2±5	10.3±4	15.3±4	12.3±4	10.2±
88.6*	6.2±4	10.3±6	5.3±3	10.2±3	6.2±3	8.3±4	4.4±4	8.2±
98.6†	3.2±2	5.6±3	6.2±4	5.2±4	4.0±2	3.0±2	5.2±3	5.8±

* D.F. = 18.
† D.F. = 16.

greatly at higher levels of homozygosity, but at lower levels, i.e., 25 per coefficients of inbreeding, there is practically no change in genetic variance fr the initial foundation population.

Relaxed selection at the lower level of inbreeding causes an increase in heritability estimates of the selected lines. At higher levels of inbreed relaxed selection has no effects on the genetic variance in the selected lines, heritability estimates remain almost constant.

Percentage emergence

Percentage emergence is calculated as the number of adults expressed in p centage of the number of eggs deposited in each vial for each line on four s cessive days. The results are presented in Figure 3.

Figure 3 shows that percentage emergence in the various selected lines affected greatly at the lower coefficients of inbreeding after which it rema almost constant throughout the experiments. In both experiments, short w selected lines showed less percentage emergence than long wing selected on which agrees with the results of most selection and inbreeding experiments Drosophila.

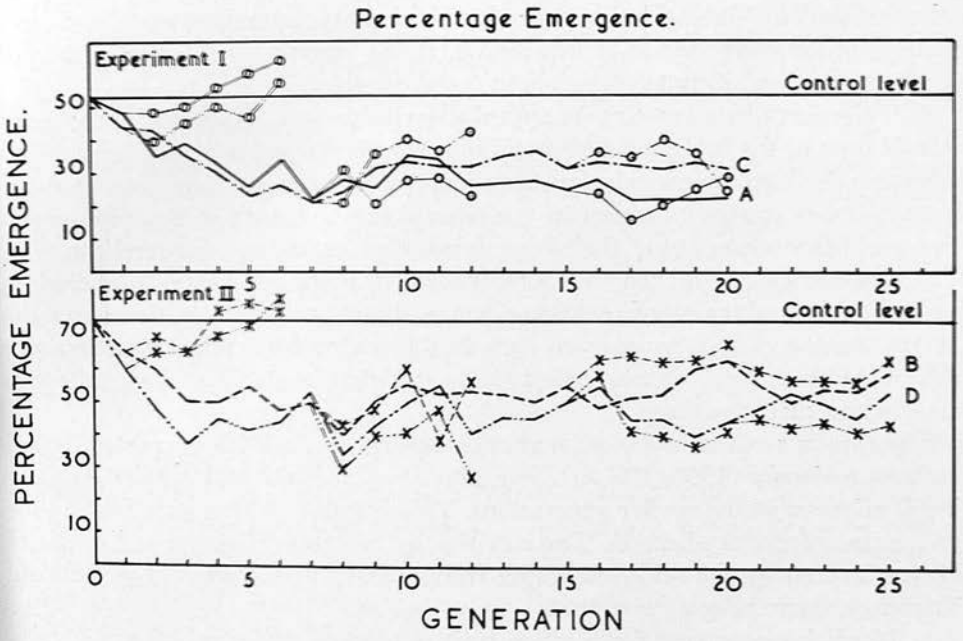

FIGURE 3.—Percentage of eggs yielding flies in the different selected lines. For symbols see Figure 1.

Relaxed selection, at lower levels of inbreeding, caused an increase in percentage emergence in all lines almost to the control level, while at higher levels of inbreeding there are practically no differences in percentage emergence between selected and relaxed lines.

SUMMARY AND CONCLUSIONS

1. Selection experiments in *Drosophila melanogaster* have been carried out with brother-sister matings for 20 and 25 generations in two identical experiments. Selection was practiced for long and short wing length and response to selection was achieved from the first generation of selection to the fourth in the long wing selected lines and to the fifth in the short wing selected lines, after which selection limits were eventually reached. Lines selected for short wing length showed higher response to selection than those selected for long wing.

2. Relaxed selected lines returned to the control level when selection was relaxed at 25 percent coefficient of inbreeding. At higher levels of inbreeding relaxed selection had no effects on the selected characters, i.e., relaxed selected lines remained almost as constant as the selected lines.

3. In all lines, thorax length behaved in the same manner as wing length with respect to all characters studied.

4. Phenotypic variation was decreased by inbreeding and selection from the first generation of selection, then ceased to decrease when body size had reached

selection limits. When selection was relaxed, phenotypic variance returned com pletely, at the lower levels of inbreeding, to the control level, while at high levels, it remained almost constant in the relaxed selected lines.

5. Selection with sibmatings cannot change the genetic variance of the selec inbred lines at the lower coefficients of inbreeding. At higher levels, heritabil estimates declined almost to insignificant values. When selection was relaxed, t heritability estimates increased in the relaxed selected lines at the lower coef cients of inbreeding; but at the higher levels such estimates remained consta

6. Percentage emergence was decreased from the first generation of inbreedi and selection, and remained constant when selection limits were achieved in va length. Such a character returned back to the control level when selection w relaxed at lower levels of inbreeding, while at higher levels, relaxed selection h no effect on such character.

The results secured in the present experiments confirm those reported by t author previously (1956a, 1957a). Selection combined with an intensive inbre ing is effective in the earlier generations. This is followed by a stabilization, the character under selection. The stabilization is achieved owing to fixatio alleles favored by the selection which were present in the original populati Therefore, it can be concluded that:

a. Much improvement for a given trait is possible under selection with s matings before homozygosity for specific combining genes is approached.

b. Limits of improvements are not likely to be reached until the segregati genes become homozygous for those alleles which combine best in the selec lines.

c. Inbreeding is the major factor in eliminating heterozygosity, while selec serves to identify the genotypes favoring the progress in the desired direct

ACKNOWLEDGMENT

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EFFECTS OF SIZE ON FECUNDITY, LONGEVITY AND VIABILITY IN POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA**

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It is well known that body size of Drosophila is determined by interaction of genetic and environmental factors. The evidence for this is derived from investigations carried out mainly on *Drosophila melanogaster* to study the inheritance of wing and thorax length which are correlated with size. The work of Robertson and Reeve (1952) and their series thereafter and Tantawy (1957 and 1959) show that variation in body size of *Drosophila melanogaster* is due more to additive genetic variance rather than to environmental variations. On the other hand, Bell, Moore and Warren (1955) and Robertson (1957) found that variations in egg production are conditioned by environmental agencies more than genetic variations. Thus the environmental conditions would seem to play a greater role in determining the egg laying capacity than the body size of an individual female. Robertson and Sang (1944a, b) reported that the rate at which eggs are laid by *Drosophila melanogaster* is very sensitive to variations in the environmental conditions of both larval and adult flies. Reeve (1954) discussed the relationship between the egg production and body size, and pointed out the need for more experimental investigations of this problem.

The present experiment was designed to study the effects of size, that is wing and thorax length, in populations of *Drosophila pseudoobscura* on lifetime egg production, longevity of adult females and viability under various environmental conditions.

TECHNICAL PROCEDURE

Two cages Nos. 3 and 6 of populations of *Drosophila pseudoobscura*, homozygous for the Arrowhead (AR/AR) gene arrangement in the third chromosome, which were maintained for about two years at 25°C. and 15°C., respectively, were used as sources of material for the present investigation.

At the beginning of the experiment, cups were taken from each cage to obtain virgin females. From each cage 200 virgin females were obtained during the first twelve hours of hatching. All virgin females were measured for wing and thorax length by the method devised by Robertson and Reeve (1952).

The technical procedure used for females obtained from cage No. 3 was carried out in the following way. Each individual female was measured and

*This work has been carried out during the tenure by the senior author of the Boese Fellowship at Columbia University, New York.

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put in a separate food vial; flies with large, medium and small wing length were then selected. The first two largest females were selected, one to be kept at 25°C. and the other at 15°C. The same procedure was used for the next two largest females, and so on for the first sixty females; that is, thirty females were selected for long wing length to lay eggs at 25°C., and another thirty females of almost the same size were selected to lay eggs at 15°C. At the same time sixty virgin females of medium size and another sixty females of small size were selected; half of each group were used for laying eggs at 25°C. and the other half at 15°C.

An exactly similar procedure was used for females obtained from cage No. 6. Measurements and selection for wing length were all done during the first twenty hours after hatching. Therefore, 360 virgin females were selected for laying eggs, thirty females in each group at each of the two temperatures.

Each selected female was mated in a separate vial to three males from the same cage; each vial contained a paper spoon with usual cream-of-wheat molasses medium with a drop of Fleischmann's yeast. Every day at 9 A.M. spoons were taken out of the vials and immediately new spoons with food and yeast were inserted in the vials. Eggs were counted on each spoon under a binocular microscope. Dead females were replaced by other females of about the same size, if possible, but only during the first ten days of their age after which no replacements were made. Spoons with counted eggs of the first ten largest females and the first ten smallest females in the large and small selected groups, were placed in food bottles. Spoons with eggs produced by an individual female for every two successive days were put in one food bottle. After hatching of the adults, flies were counted and classified as to sex. Such counting was made first two days after hatching, and thereafter once every five days for two weeks.

All adult females used for laying eggs and the culturing of eggs in food bottles were treated similarly to assure the same environmental conditions under all temperatures. The grand total number of eggs counted in the present work was 384,965 eggs, for all groups under the two temperatures.

RELATION BETWEEN SIZE AND LIFETIME EGG PRODUCTION

The relationship between females with large, medium and small wing length, and the capacity for laying eggs during the lifetime at different temperatures is reported in figures 1 and 2, for 25°C. and 15°C., respectively. The results are presented as averages per day on a given week. No eggs were laid during the first two days of the adult female life at 25°C., and for the first four days at 15°C.

The results reported in figures 1 and 2 show clearly the effects of size on lifetime egg production; larger females lay more eggs than medium or small ones at both temperatures. The average daily productivity per week increases rapidly after the first week at 25°C. and somewhat more slowly at 15°C. The period of high egg production varies considerably with temperature, but is uniform for flies of different sizes. At 25°C. the highest

FIGURE
wing

FIGURE
wing

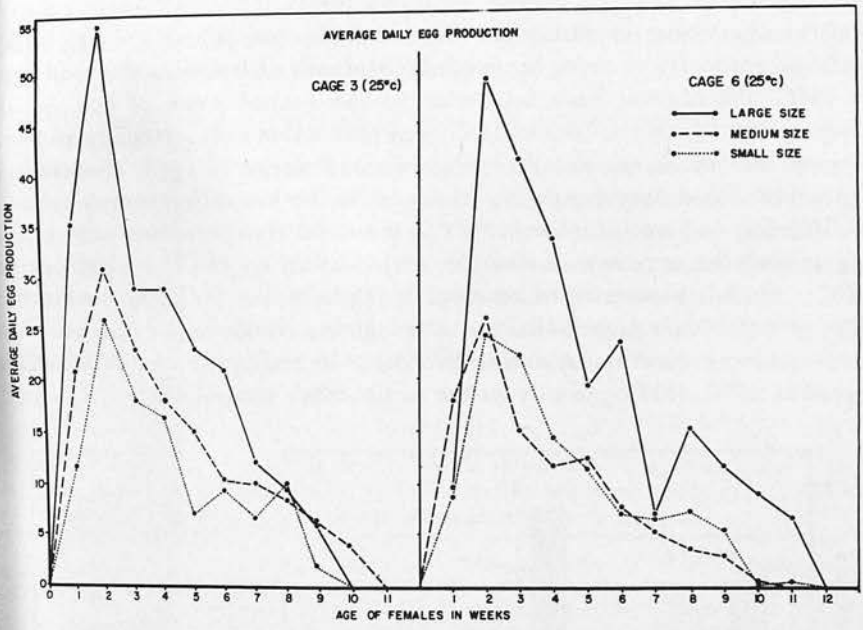

FIGURE 1. Lifetime egg production for large, medium and small selected females for wing length at 25°C. Each point represents the daily average on a given week.

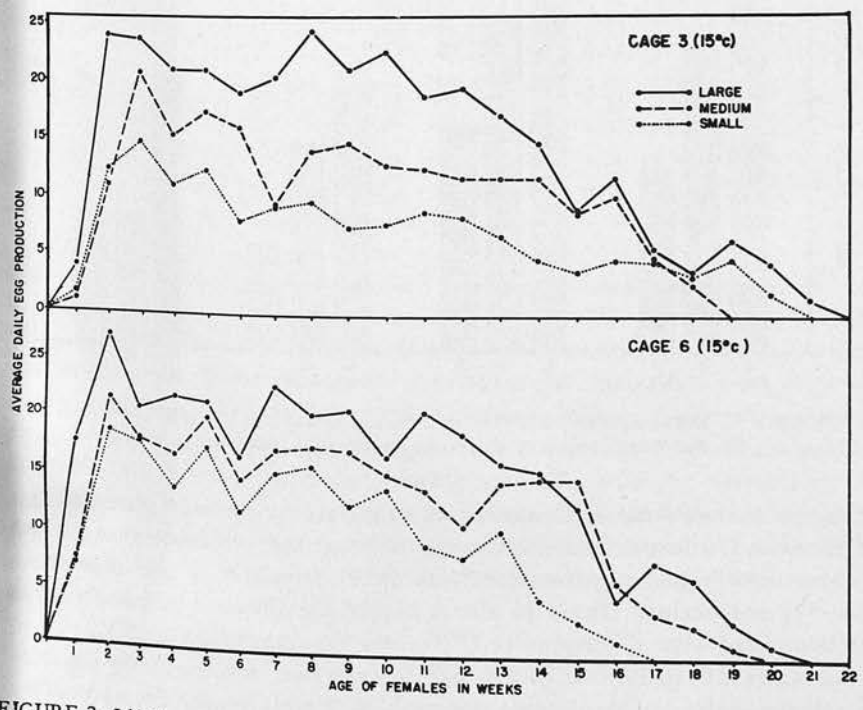

FIGURE 2. Lifetime egg production for large, medium and small selected females for wing length at 15°C. Each point represents the daily average on a given week.

peak of egg laying is during the second week, after which the egg laying declines gradually to zero, between the eleventh and twelfth weeks of age. At 15°C. the highest peak falls also on the second week of life for all groups, after which the decline in the egg production goes gradually to zero, between the twentieth and the twenty-second weeks of age. The average egg production during the peak periods under the two different temperatures is different, and much higher at 25°C. It can be also noted that most of the egg production occurs at an earlier period at 25°C. and at a later one at 15°C. Similar results were reported by Dobzhansky (1935) on unselected flies of *Drosophila pseudoobscura*, although our results differ from his with respect to the duration of active lifetime. In his experiment, the females reared at 25°C. laid eggs only as far as the sixth week of age.

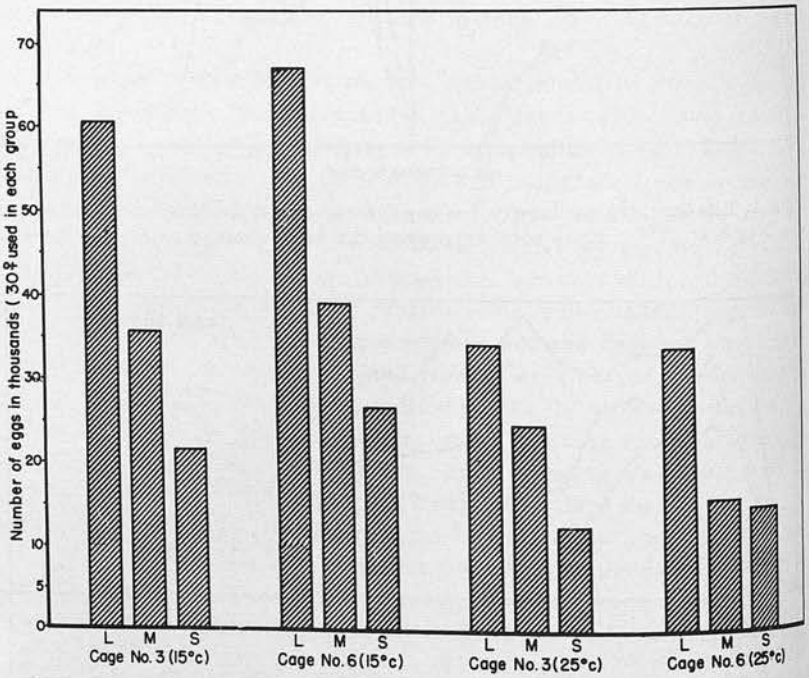

FIGURE 3. Total ovaposition rate in relation to size of the selected females for wing length at different degrees of temperature.

Figure 3 shows the total number of eggs laid by the same total numbers of females (30 females in each group) kept at the two temperatures. The results show highly significant effects of the female body size on the lifetime egg production. There is also a highly significant difference between the two temperatures; females at 15°C. laid more eggs than at 25°C.

Spiess (1958) found that in *Drosophila persimilis* the egg laying capacity of females raised under conditions of high larval density does not differ significantly from that of females raised under near optimal conditions. It is well known from the results reported by many investigators, for ex-

ample, Sang (1950) that larval crowding affects the size of the resulting flies, that is, the flies hatched from crowded cultures are smaller in size than those from optimally populated ones.

PHENOTYPIC VARIATIONS OF BODY SIZE AND EGG PRODUCTION

Phenotypic variations of the body size and the egg production are calculated as coefficients of variation, and the results are presented in table 1, which shows that the coefficients of variation for the egg production are much higher than those for body size. This indicates that the former character is affected by environmental conditions more than the latter one. Robertson and Reeve (1955) found that the relative variance of the fecundity of *Drosophila melanogaster* is about 200 times as that for body size. They

TABLE 1

Total lifetime egg production per female in relation to wing length and thorax length. Means are presented with their respective standard errors (S.E.) and coefficients of variation (C.V.). Units of measurement are of $^1/_{100}$ mm.

Cage No.	Temperature	Size	Wing length		Thorax length		Egg production	
			Mean ± S.E.	C.V.%	Mean ± S.E.	C.V.%	Mean ± S.E.	C.V.%
3	25°C.	Large	217.47 ± 1.56	2.58	104.09 ± 0.94	3.27	1131.69 ± 146.61	46.64
		Medium	198.63 ± 2.23	5.61	94.32 ± 1.32	6.99	822.32 ± 80.36	48.86
		Small	180.03 ± 3.52	6.05	83.64 ± 2.10	7.70	409.20 ± 85.23	64.57
6	25°C.	Large	232.22 ± 2.53	3.49	106.59 ± 1.06	3.10	1127.90 ± 142.09	40.31
		Medium	211.77 ± 2.51	4.39	99.59 ± 1.73	6.43	512.14 ± 108.57	78.44
		Small	182.50 ± 3.78	7.45	86.70 ± 1.47	6.11	502.23 ± 125.22	89.77
3	15°C.	Large	217.46 ± 2.50	3.91	105.10 ± 1.68	5.42	2021.00 ± 72.35	12.17
		Medium	201.84 ± 2.10	4.16	95.96 ± 1.28	5.31	1174.19 ± 132.45	45.12
		Small	173.86 ± 2.00	3.80	81.91 ± 1.88	7.57	726.73 ± 8.75	39.73
6	15°C.	Large	233.15 ± 2.61	3.69	107.84 ± 1.42	4.36	1894.73 ± 319.75	55.69
		Medium	206.47 ± 4.42	8.14	99.17 ± 2.82	10.79	974.27 ± 183.71	71.73
		Small	187.77 ± 3.88	6.82	90.45 ± 2.30	8.40	890.27 ± 230.03	85.22

also reported that inbreeding causes a decline in the egg production and the size; the latter is, however, relatively less affected than the former. The egg production may be regarded as more sensitive than the body size with respect both of environmental and genetical changes. Our results indicate that changes in environmental conditions cause changes in egg production and its variability; at 25°C. the egg production is much lower than at 15°C., the latter temperature showing less affect on the variability. A similar difference is observed between large and small flies, the egg production of the former is less variable than that of the latter. These results are in agreement with those reported by Gowen and Johnson (1946) for *Drosophila melanogaster.*

LONGEVITY AND LIFETIME EGG PRODUCTION

Table 2 shows the relationship between wing length, the longevity, and the average daily egg production. The selection differentials are measured

as differences between the wing length in the selected females and the population mean from which they were selected. The results show that the higher averages of egg production are associated with higher selection differentials for female wing length and for her longevity. In all cases larger females live longer and produce more eggs than smaller or medium ones. It could, therefore, be concluded that the metabolic activity as measured by egg production capacity is correlated with the physiological fitness as measured by female capacity to survive. These results are in agreement with those reported by Dobzhansky (1935).

Table 2 illustrates that the daily average egg production is higher at 25°C. than at 15°C., but the total lifetime egg production (figure 3) is much higher at the latter temperature than at the former. Such differences are due to the fact that adult females live longer at a lower temperature than at a higher one.

TABLE 2

Average daily egg production per an individual female in relation to selection differential (S.D.) for female wing length and longevity of adult females. Standard errors (S.E.) for means are also presented. Units of measurements are of $^1/_{100}$ mm.

Cage No.	Temperature	Size	S.D. ± S.E.	Average daily egg production ± S.E.	Average longevity ± S.E. (Days)
3	25°C.	Large	21.68 ± 1.58	24.51 ± 1.41	37.31 ± 5.44
		Medium	2.83 ± 2.22	14.78 ± 1.27	35.20 ± 3.50
		Small	−15.77 ± 3.68	12.57 ± 1.24	28.20 ± 5.13
6	25°C.	Large	25.19 ± 2.64	20.93 ± 2.08	36.30 ± 6.53
		Medium	4.78 ± 2.51	10.78 ± 1.22	35.18 ± 4.30
		Small	−23.66 ± 3.44	10.53 ± 1.08	31.53 ± 9.88
3	15°C.	Large	21.67 ± 2.50	15.03 ± 0.76	119.12 ± 6.50
		Medium	6.04 ± 2.10	10.79 ± 0.57	95.00 ± 6.43
		Small	−21.94 ± 2.06	7.33 ± 1.36	83.45 ± 9.91
6	15°C.	Large	26.14 ± 2.58	17.82 ± 0.81	92.91 ± 11.45
		Medium	0.53 ± 4.42	15.18 ± 0.63	80.13 ± 6.26
		Small	−19.23 ± 3.88	12.79 ± 0.64	70.00 ± 10.69

It is of interest to note from table 2 and figure 3 that the original temperature of the population may have an influence on the capacity for laying eggs. Females from cage No. 3 were reared at 25°C. However, egg production at 15°C. is different; females from cage six show a higher egg production. These results are in agreement with those reported by Tantawy and Mallah (1961) who worked on natural populations of *Drosophila melanogaster* and *D. simulans* and found that the temperature prevailing in various geographical regions affect the body size and the egg viability.

VIABILITY AND SEX-RATIO

The viability is measured as the percentage emergence of adults that hatched from a given number of eggs cultured in ordinary food bottles. Table 3 reports for ten females in each of the selected groups the total

lifetime egg production and the percentage of emergence and sex-ratio of the progeny. Size of the female parent has no significant effect on the percentage of her eggs which successfully develop to adult stage. The results do, however, indicate differences between the two temperatures; 15°C. shows a higher viability. The sex-ratios of the various groups are uniform; females slightly out-number the males.

TABLE 3

Lifetime egg production (ten females in each selected group) cultured in food bottles, with percentages of the emergence of adult flies and the sex-ratio

Cage No.	Temperature	Size	Total lifetime egg production	No. of hatched		Per cent of emergence	Sex-ratio*
				Males	Females		
3	25°C.	Large	14,712	5,002	5,293	69.97	51.41
		Small	4,967	1,642	1,800	69.29	62.29
6	25°C.	Large	11,279	3,969	4,207	72.54	51.45
		Small	6,259	2,132	2,304	70.89	51.93
3	15°C.	Large	24,257	9,704	10,171	81.91	51.16
		Small	7,944	3,213	3,405	83.30	51.15
6	15°C.	Large	20,842	8,283	8,574	80.88	50.21
		Small	9,793	4,082	4,097	83.51	50.09

*Percentage of females to males.

CONCLUSIONS

The present study, on populations of *Drosophila pseudoobscura*, shows that temperature has a highly significant effect on the egg production. Females lay more eggs at a low than at a high temperature. This agrees with the data of Alpatov (1932) on *Drosophila melanogaster* and of Dobzhansky (1935) on *Drosophila pseudoobscura*.

Robertson (1957) reported that body size of *Drosophila melanogaster* may influence egg laying capacity. Our results on the whole agree with Robertson's results, but the present work indicates a highly significant effect of the female body size on the capacity for egg laying, and on the longevity of the females. Alpatov (1929) and Sang (1950) have found that small flies which hatch in crowded cultures lay fewer eggs. However, Spiess (1958) reported different results.

The highly significant correlations found between body size and egg production may indicate that these two characters are genetically correlated. The available data do not warrant such a conclusion, but it would be interesting to investigate experimentally this problem in *Drosophila pseudoobscura*. Robertson (1957) found in his selection experiment for size in *Drosophila melanogaster* that only in one comparison, after five generations of selection, was there evidence of correlation between size and egg production; in the others the difference in the egg output of large, small and unselected groups were negligible. He concluded that a substantial change in body size by selection does not lead to parallel changes in egg produc-

tion. Our results indicate that changes in body size of *Drosophila pseudoobscura* are accompanied by changes in egg production. This statement needs to be clarified by more experimental studies on selection for large and small sizes and lifetime egg production at different generations of selection.

Results obtained clearly show that size has a great influence on egg production, on longevity of adult females, but not on egg viability. This indicates that egg viability is a character which depends entirely on parental genotype rather than their phenotypes.

SUMMARY

1. An experiment was designed to test the effects of body size in *Drosophila pseudoobscura* on lifetime egg production, longevity, and egg viability.

2. The results show that large females lay significantly more eggs than medium or small flies; small females lay the least number of eggs. Comparing the egg laying capacity at different temperatures, it is found that females at 15°C. lay more eggs than those at 25°C.

3. Larger females live longer than medium or small flies: the longevity of adult females kept at 15°C. is greater than at 25°C.

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Note: For more statistical analyses applying the path coefficient theory to the present data, see Tantawy, 1961, Genetics, Vol. 46, No. 1 (in press).

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EFFECTS OF TEMPERATURE ON PRODUCTIVITY AND GENETIC VARIANCE OF BODY SIZE IN POPULATIONS OF DROSOPHILA PSEUDOOBSCURA[1]

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HERITABILITY of body size, i.e., wing and thorax length, has been thoroughly studied by ROBERTSON and REEVE (1952) and TANTAWY (1959) working on *Drosophila melanogaster*. They reported that the heritability of wing length ranged between 30–40 percent. No estimates for body size on other species of Drosophila have been made.

The most important factors that may affect the additive genetic variance of a given character are selection and inbreeding. The effects of selection depend greatly on the parental relationship. Mating between remote relatives causes an increase (REEVE and ROBERTSON 1953; TANTAWY 1956), while that between full sibs causes a decline (TANTAWY 1959). Inbreeding with random mating is the major factor decreasing the additive genetic variance, and the extent to which this may happen depends on closeness of relationship of individuals. TANTAWY and REEVE (1956) and TANTAWY (1957a) reported that matings between full sibs are most effective in depleting the original heterozygosity for a given character, while crossing highly inbred lines (TANTAWY 1957b) leads to increase.

The present investigation was carried out to study the heritability estimates for body size, i.e., wing and thorax length, in populations of *Drosophila pseudoobscura* and the influence of the original temperature conditions on such estimates.

TECHNICAL PROCEDURE

Two cages, Nos. 3 and 6 of populations of *Drosophila pseudoobscura* homozygous for the Arrowhead (*AR/AR*) gene arrangement in the third chromosome, were the material of the present study. The cages were maintained for two years at 25°C and 15°C, respectively. From each cage, 200 virgin females were measured for wing and thorax length, and selection was carried out for large, medium and small wing length. Thirty females from each selected group were used for laying eggs for their lifetime at 25°C and at 15°C. For more details concerning measuring of adult females, methods of selection and egg counting, see TANTAWY and VETUKHIV (1960).

Eggs from the first ten largest females and the first ten smallest females of the

[1] The present work has been carried out during the tenure of the author of the Boese Fellowship at the Department of Zoology, Columbia University, N.Y., U.S.A.

large and small selected groups were cultured in food bottles. Wing and thorax length of the offspring of both sexes that hatched on the first two days were measured. On each day five males and five females were measured, i.e., 200 pairs of flies were used in each of the selected groups. At the same time a control stock kept in mass matings from each cage was maintained under each temperature and given the same treatment as those of the selected parents. Twenty pairs of flies, on the same two days, were measured from each of the control stocks. Methods recommended by ROBERTSON and REEVE (1952) for measuring wing length and control of environmental variations were followed.

Effect of size on the productivity under various temperatures: The correlation coefficients between parental female size, at various degrees of temperature, and lifetime egg production and longevity are presented in Table 1.

TABLE 1

Phenotypic correlation coefficients between wing length (W) *of the parental females, thorax length* (T), *lifetime egg production* (G) *and longevity* (L), *with their standard errors. Degrees of freedom=89*

Correlation coefficients between	25°C		15°C	
	Cage no. 3	Cage no. 6	Cage no. 3	Cage no. 6
Female wing length and:				
Female thorax length (r_{WT})	0.850 ± 0.029	0.865 ± 0.027	0.941 ± 0.012	0.899 ± 0.020
Egg production (r_{WG})	0.506 ± 0.079	0.263 ± 0.099	0.540 ± 0.075	0.323 ± 0.095
Longevity (r_{WL})	0.143 ± 0.104	0.233 ± 0.100	0.340 ± 0.094	0.267 ± 0.099
Female thorax length and:				
Egg production (r_{TG})	0.621 ± 0.065	0.313 ± 0.096	0.580 ± 0.070	0.369 ± 0.092
Longevity (r_{TL})	0.283 ± 0.088	0.296 ± 0.097	0.436 ± 0.086	0.326 ± 0.096
Egg production and:				
Longevity (r_{GL})	0.728 ± 0.049	0.558 ± 0.073	0.737 ± 0.048	0.763 ± 0.044

The path coefficient theory of WRIGHT (1921a,b, 1923, 1934) was applied to the correlations in Table 1. The points that need to be taken into consideration are:

A. Egg production may be influenced by longevity.

B. Wing and thorax length are influenced by genetic and environmental factors.

C. The genetic factors for body growth may well influence the rate of lifetime egg production positively. Common genetic factors for body growth and longevity seem less probable though not, of course, impossible.

D. Aspects of favorable environmental conditions on body growth may be expected to be favorable also for longevity and for rate of egg production.

One and two factor hypotheses: From Table 1 it can be seen that there are significant differences among the sets in all the correlations except r_{WL} and r_{TL}. There seems to be some tendency toward higher correlations at 15°C than at 25°C, and perhaps some tendency for Cage 3 to show higher correlations than Cage 6, but neither difference is constant. There is enough similarity among the

four sets to make it seem worthwhile to get a single over-all picture from the average correlations. The statistical analyses for all four populations and the set of average correlations are shown in Table 2.

The analysis on the basis of a single common factor requires that thorax length be an almost perfect indicator of the general size. Factor S shows a strong effect on wing at all temperatures, but shows rather varied influence on lifetime egg production. Results are shown in the calculated path coefficients of Table 2. Effects of S on egg production through its effect on longevity are: 0.140 and 0.144 for females of Cages 3 and 6, respectively, which were maintained at 25°C. The corresponding figures for the cages kept at 15°C are: 0.240 and 0.223, respectively. Such results indicate clearly that factor S affects life egg production by this route more at a colder temperature than at a warmer one.

On calculating the correlations from the estimated path coefficients r_{WT}, r_{TG} and r_{GL} agree exactly while, as noted, small deviations from the observed values are shown in the other three. Only in the case of the first population (A) is the deviation as much as half the standard error. This solution must thus be considered as a possible one. The fact that it fits reasonably well does not, however, prove that it is correct. It would, indeed, be very surprising if wing (W), thorax (T) and egg production (G) were acted upon by all factors (genetic and environmental) in such closely parallel fashion that these factors could be combined accurately into one (S_1). Diagram 1, which is based on the average of all four populations, illustrates the effects of such a factor. S_1 affects all four different characters independently and also affects (G) through (L). Such a diagram indicates that the contribution to the correlation of (W) with (G) through (S_1) alone is 0.252 and that through S_1 and (L) is 0.166, which give a total correlation coefficient (r_{WG}) of 0.418. The corresponding figures for the contributions to the correlations of (T) with (G) are: 0.285 and 0.186, respectively, totalling 0.471, which indicate that (W) and (T) show rather similar relations to the egg production rate.

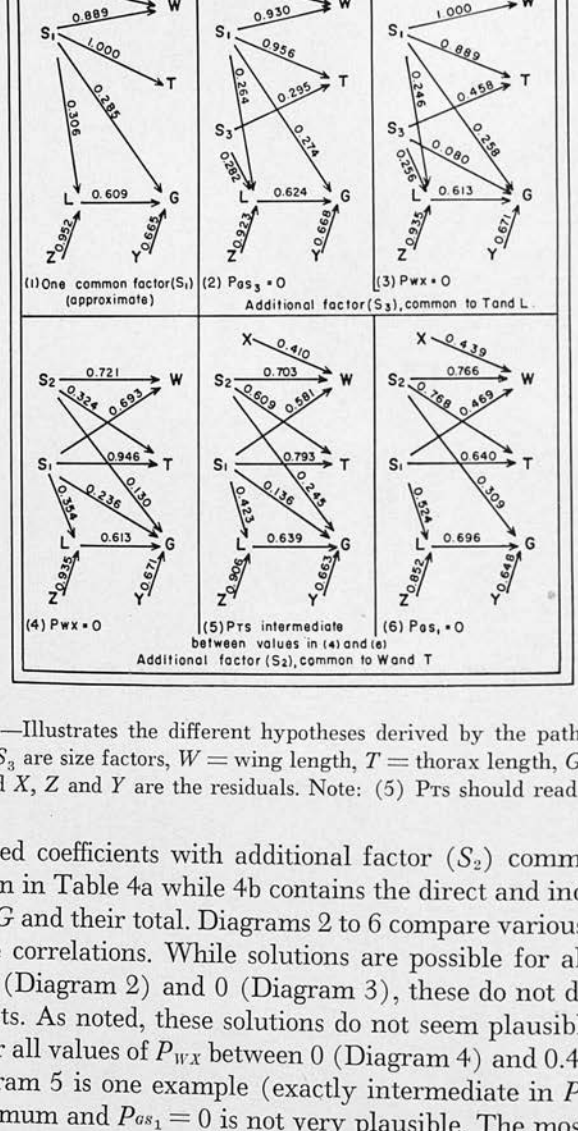
A two factor solution introduces too many paths for a unique solution. It is of interest, however, to find the range of possible solutions. Consideration of equation (11) in Table 2, shows that exact solution may be obtained either by introducing an additional factor common to (W) and (T) or one common to (T) and (G), while an additional one common to (W) and (G) would make the fit worse. The same conclusion follows on making the calculations from equations (1), (3) and (5) instead of equations (1), (2) and (4). It seems better to postulate a factor (S_2) common to wing and thorax, than one (S_3) common to thorax and egg production. However, the latter was also tried out. A unique solution can be obtained (by iteration) by assuming that egg production is related to the additional factor (S_3) only through longevity $(P_{GS_3} = 0)$ as shown in Diagram 2. Another unique solution can be obtained by making P_{GS_3} as large as possible without making S_{WX} impossible $(P_{WX} = 0)$ as shown in Diagram 3. The solutions for the average of correlations under both of these assumptions are reported in Table 3. Such results seem to be of interest only as mathematically possible solutions, rather than as physiologically probable ones.

TABLE 2

Statistical analyses, for correlations of Table 1, for all four different populations and the set of average correlations

Item	25°C A Cage no. 3	25°C B Cage no. 6	15°C C Cage no. 3	15°C D Cage no. 6	Average correlations
(1) $r_{WT} = P_{WS} P_{TS}$	0.850	0.865	0.941	0.899	0.889
(2) $r_{WG} = P_{WS} r_{GS}$	0.506(0.528)	0.263(0.271)	0.540(0.546)	0.323(0.332)	0.408(0.418)
(3) $r_{WL} = P_{WS} P_{LS}$	0.143(0.192)	0.233(0.244)	0.340(0.375)	0.267(0.279)	0.246(0.272)
(4) $r_{TG} = P_{TS} r_{GS}$	0.621	0.313	0.580	0.369	0.471
(5) $r_{TL} = P_{TS} P_{LS}$	0.283(0.226)	0.296(0.283)	0.436(0.399)	0.326(0.311)	0.335(0.306)
(6) $r_{GL} = P_{GL} + P_{GS} P_{LS}$	0.728	0.558	0.737	0.763	0.696
(7) $P_{WS}/P_{TS} = (2)/(4)$	0.815	0.839	0.931	0.874	0.866
(8) $P_{WS}/P_{TS} = (3)/(5)$	0.503	0.786	0.780	0.819	0.732
(7) and (8) are inconsistent (especially in A, less in C, only slightly in B and D)					
(7) based on the larger correlations will be used to obtain an approximate solution					
(9) $P^2_{WS} = (1) \times (7)$	0.693	0.726	0.876	0.787	0.770
(10) $P_{WS} = \sqrt{(9)}$	0.832	0.852	0.936	0.887	0.878
(11) $P_{TS} = (1)/(10)$	1.022	1.015	1.005	1.015	1.013
It is impossible for P_{TS} to exceed 1.0 under the postulated system of relations. It is, however, remarkable that all populations give values so close to 1.0. A good approximation should be obtained from $P_{TS} = 1.0$.					
(12) P_{WS} (revised) $= (1)$ if $P_{TS} = 1.000$	0.850	0.865	0.941	0.899	0.889
(13) $P_{LS} = (3)/(12)$	0.168	0.269	0.362	0.296	0.276
(14) $P_{LS} = (5)$	0.283	0.296	0.436	0.326	0.335
(13) and (14) reflect the inconsistency of (8) with (7). The average will be used.					
(15) P_{LS} (average) $= \frac{1}{2}[(13) + (14)]$	0.226	0.283	0.399	0.311	0.306
(16) $r_{GS} = r_{TG} = P_{GS} + P_{LS} P_{GL}$	0.621	0.313	0.580	0.369	0.471
(17) $P_{GL}(1 - P^2_{LS}) = (6) - (15)(16)$	0.588	0.469	0.505	0.648	0.552
(18) $P_{GL} = (17)/[1 - (15)^2]$	0.619	0.509	0.601	0.718	0.609
(19) $P_{GS} = (16) - (15)(18)$	0.482	0.169	0.340	0.146	0.289
Calculated path coefficients					
$P_{WS} = (12)$	0.850	0.865	0.941	0.899	0.889
$P_{WX} = \sqrt{1 - (12)^2}$	0.526	0.502	0.339	0.436	0.458
P_{TS} see (11)	1.000	1.000	1.000	1.000	1.000
$P_{GS} = (19)$	0.482	0.169	0.340	0.146	0.285
$P_{GL} = (18)$	0.619	0.509	0.601	0.718	0.609
$P_{GY} = \sqrt{1 - (19)(16) - (18)(6)}$	0.500	0.814	0.600	0.631	0.665
$P_{LS} = (15)$	0.226	0.283	0.399	0.311	0.306
$P_{LZ} = \sqrt{1 - (15)^2}$	0.974	0.959	0.917	0.950	0.952

On substituting in (1) to (6), using $r_{GS} = r_{TG} = (4)$; (1), (4) and (6) agree perfectly with the observed correlations while (2), (3) and (5) come out as indicated in parentheses. The deviations are all small compared with the standard error (which are largest in (3), next in (5) and next to this in (2)).



DIAGRAMS 1–6.—Illustrates the different hypotheses derived by the path coefficient theory, where S_1, S_2 and S_3 are size factors, W = wing length, T = thorax length, G = egg production, L = longevity and X, Z and Y are the residuals. Note: (5) P_{TS} should read (5) P_{TS_1}.

The calculated coefficients with additional factor (S_2) common to wing and thorax are given in Table 4a while 4b contains the direct and indirect paths connecting T and G and their total. Diagrams 2 to 6 compare various solutions based on the average correlations. While solutions are possible for all values of P_{WX} between 0.367 (Diagram 2) and 0 (Diagram 3), these do not differ very much in other respects. As noted, these solutions do not seem plausible. Solutions are also possible for all values of P_{WX} between 0 (Diagram 4) and 0.439 (Diagram 6) of which Diagram 5 is one example (exactly intermediate in P_{TS_1}). Diagram 6 with P_{GS_2} maximum and $P_{GS_1} = 0$ is not very plausible. The most plausible solution is probably somewhere between Diagrams 4 and 5. The former does not differ very much from Diagram 1, except in postulating that the residual factor for *(W)*, (here S_2), has small effects on *(T)* and *(G)* instead of being restricted to action on *(W)*, (factor x).

Heritability of wing and thorax length: It is of interest to relate heritability estimates to the set of path coefficients. This can be done if we take Diagram 4 or 5 as the most plausible and use the same diagram for both parent and offspring (which may not be wholly justified) and if then we determine what the parent-offspring correlation would be on the assumption of no dominance or interaction,

TABLE 3

Illustrates the various correlation coefficients between different characters as well as path coefficients on the assumptions that $P_{GS_3} = 0$ *and* $P_{WX} = 0$. *The approximate one factor (No* S_3*) is given for comparison*

Correlations	Average correlations
$r_{WT} = P_{WS_1} P_{TS_1}$	0.889
$r_{WG} = P_{WS_1} r_{GS_1}$	0.408
$r_{WL} = P_{WS_1} P_{LS_1}$	0.246
$r_{TG} = P_{TS_1} r_{GS_1} + P_{TS_3} r_{GS_3}$	0.471
$r_{TL} = P_{TS_1} P_{LS_1} + P_{TS_3} P_{LS_3}$	0.335
$r_{GL} = P_{GL} + P_{GS_1} P_{LS_1} + P_{GS_3} P_{LS_3}$	0.696
$r_{GS_1} = P_{GS_1} + P_{GL} P_{LS_1}$	
$r_{GS_3} = P_{GS_3} + P_{GL} P_{LS_3}$	
$r_{WW} = P^2_{WS_1} + P^2_{WX}$	1.000
$r_{TT} = P^2_{TS_1} + P^2_{TS_3}$	1.000
$r_{GG} = P_{GS_1} r_{GS_1} + P_{GS_3} r_{GS_3} + P_{GL} r_{GL} + P^2_{GY}$	1.000
$r_{LL} = P^2_{LS_1} + P^2_{LS_3} + P^2_{LZ}$	1.000

	No S_3 One factor (approximate)	$P_{GS_3} = 0$	$P_{WX} = 0$
P_{WS_1}	0.889	0.930	1.000
P_{WX}	0.458	0.367	0
P_{TS_1}	1.000	0.956	0.889
P_{TS_3}	0	0.295	0.458
P_{GS_1}	0.285	0.274	0.258
P_{GS_3}	0	0	0.079
P_{GL}	0.609	0.624	0.613
P_{GY}	0.665	0.668	0.671
P_{LS_1}	0.306	0.264	0.246
P_{LS_3}	0	0.282	0.256
P_{LZ}	0.952	0.923	0.935
r_{GS_1}	0.471	0.439	0.408
r_{GS_3}	0	0.176	0.236

Two solutions on the assumption of a factor, (S_3), common to T and L in addition to one, (S_1), common to W, T and L. One solution is obtained by assuming that $P_{GS_3} = 0$, the other by assuming that $P_{WX} = 0$. Intermediate solutions can be obtained, without giving any negative values, by taking values of P_{GS_3} between zero and 0.0799. The approximate one factor solution (No S_3) is given for comparison (see Table 2).

plus the further assumptions that S_2 is wholly genetic and S_1 wholly environmental in Diagram 4, or S_2 and S_X are wholly genetic and S_1 environmental in Diagram 5. The results are presented in Diagram 7a and b. Diagram 7a gives a fairly good result for $r_{w_o w_p}$ but too small a result for $T_o T_p$, while Diagram 7b gives considerably too large a result in both cases. A system differing slightly from (a) in the direction of (b) would give the closest fit. There are, however, a good many assumptions made, and it may be doubted whether one is justified in doing more than give the heritabilities as twice the observed parent-offspring correlations on the assumption of no dominance and interaction. Table 5 shows

TABLE 4

(a) The calculated coefficients with an additional factor (S_2) common to wing and thorax for the four different populations and their averages

Item	25°C A Cage no. 3	25°C B Cage no. 6	15°C C Cage no. 3	15°C D Cage no. 6	Average correlations
$r_{WT} = P_{WS_1} P_{TS_1} + P_{WS_2} P_{TS_2}$	0.850	0.865	0.941	0.899	0.889
$r_{WG} = P_{WS_1} r_{GS_1} + P_{WS_2} P_{GS_2}$	0.506	0.263	0.540	0.323	0.408
$r_{WL} = P_{WS_1} P_{LS_1}$	0.143	0.233	0.340	0.267	0.246
$r_{TG} = P_{TS_1} r_{GS_1} + P_{TS_2} P_{GS_2}$	0.621	0.313	0.580	0.369	0.471
$r_{TL} = P_{TS_1} P_{LS_1}$	0.283	0.296	0.436	0.326	0.335
$r_{GL} = P_{GS_1} P_{LS_1} + P_{GL}$	0.728	0.558	0.737	0.763	0.696
$r_{GS_1} = P_{GS_1} + P_{GL} P_{LS_1}$					
$r_{WW} = P^2_{WS_1} + P^2_{WS_2} + P^2_{WX}$	1.000	1.000	1.000	1.000	1.000
$r_{TT} = P^2_{TS_1} + P^2_{TS_2}$	1.000	1.000	1.000	1.000	1.000
$r_{GG} = P_{GS_1} r_{GS_1} + P^2_{GS_2} + P_{GL} r_{GL} + P^2_{GY}$	1.000	1.000	1.000	1.000	1.000
$r_{LL} = P^2_{LS_1} + P^2_{LZ}$	1.000	1.000	1.000	1.000	1.000

	$P_{GS_1}=0$	Int.	$P_{WX}=0$	$P_{GS_1}=0$	Int.	$P_{WX}=0$	$P_{GS_1}=0$	Int.	$P_{WX}=0$	$P_{GS_1}=0$	Int.	$P_{WX}=0$	$P_{GS_1}=0$	Int.	$P_{WX}=0$
P_{WS_1}	0.254	0.337	0.419	0.432	0.604	0.776	0.566	0.635	0.705	0.590	0.698	0.805	0.469	0.581	0.693
P_{WS_2}	0.837	0.841	0.908	0.751	0.626	0.630	0.771	0.729	0.709	0.684	0.583	0.593	0.766	0.703	0.721
P_{WX}	0.485	0.423	0	0.499	0.493	0+	0.294	0.254	0+	0.428	0.416	0	0.439	0.410	0
P_{TS_1}	0.506	0.670	0.835	0.550	0.769	0.988	0.725	0.814	0.904	0.721	0.832	0.983	0.640	0.793	0.946
P_{TS_2}	0.863	0.742	0.551	0.835	0.639	0.156	0.689	0.581	0.428	0.693	0.524	0.183	0.768	0.609	0.324
P_{GS_1}	0	0.196	0.333	0	0.094	0.159	0+	0.129	0.229	0+	0.071	0.129	0	0.136	0.236
P_{GS_2}	0.481	0.414	0.307	0.178	0.136	0.033	0.376	0.317	0.234	0.175	0.132	0.046	0.309	0.245	0.130
P_{GL}	0.728	0.645	0.615	0.558	0.522	0.509	0.737	0.668	0.626	0.763	0.736	0.721	0.696	0.639	0.614
r_{GY}	0.489	0.517	0.527	0.811	0.814	0.815	0.562	0.588	0.602	0.622	0.629	0.633	0.648	0.663	0.671
P_{LS_1}	0.561	0.423	0.339	0.538	0.385	0.299	0.602	0.536	0.483	0.452	0.382	0.331	0.524	0.423	0.354
P_{LZ}	0.828	0.906	0.941	0.843	0.923	0.954	0.799	0.844	0.876	0.892	0.924	0.944	0.852	0.906	0.935
r_{GS_1}	0.408	0.468	0.542	0.300	0.295	0.312	0.443	0.487	0.531	0.345	0.352	0.367	0.365	0.406	0.453

(b) Direct and indirect paths connecting T *and* G *and their total (assuming factor* S_2*)*

$P_T(S_1)G = P_{TS_1} P_{GS_1}$	0	0.131	0.278	0	0.072	0.157	0	0.105	0.207	0	0.061	0.126	0	0.108	0.224
$P_T(S_1L)G = P_{TS_1} P_{GL} P_{LS_1}$	0.206	0.183	0.174	0.165	0.154	0.151	0.321	0.291	0.273	0.249	0.239	0.235	0.233	0.214	0.205
Total $= P_{TS_1} r_{GS_1}$	0.206	0.314	0.452	0.165	0.226	0.308	0.321	0.396	0.480	0.249	0.300	0.361	0.233	0.322	0.429
$P_T(S_2)G = P_{TS_2} P_{GS_2}$	0.415	0.307	0.169	0.148	0.087	0.005	0.259	0.184	0.099	0.121	0.069	0.008	0.238	0.149	0.042
r_{TG}	0.621	0.621	0.621	0.313	0.313	0.313	0.579	0.580	0.580	0.369	0.369	0.369	0.471	0.471	0.471

TABLE 5

Phenotypic correlation coefficients between parental body size and offspring size. Heritability of wing and thorax length are also given

Item	25°C		15°C	
	Cage no. 3	Cage no. 6	Cage no. 3	Cage no. 6
Correlations				
W_pW_o	0.240	0.189	0.203	0.206
T_pT_o	0.111	0.121	0.101	0.126
Heritabilities				
h^2_W	0.480	0.378	0.406	0.412
h^2_T	0.222	0.242	0.202	0.252

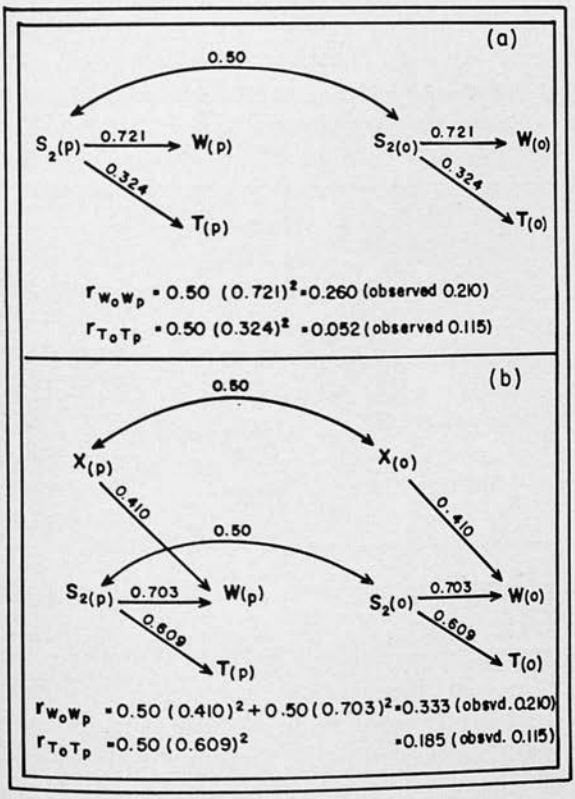


DIAGRAM 7.—Illustrates the relationship between parent and offspring size. For symbols see Diagram 1.

the phenotypic correlation coefficients between parental and offspring size; heritability of wing and thorax length are also reported. The results, as presented in Table 5, indicate that wing and thorax length of *Drosophila pseudoobscura* possess a considerable amount of additive genetic variance under any given temperature with insignificant differences between various degrees.

The results indicate that with changes in the original temperature heritability

estimates decline. The percentage decrease in the heritability estimates for wing length are 15.9 percent and 8.3 percent for Cage nos. 3 and 6, respectively. Such results indicate that the additive genetic variance of a given trait may be affected more by changing temperature from warm to cold conditions, rather than the reverse situation.

Relation between parental female size and offspring size: It has been shown by various investigators that selection of parents for wing length and thorax length has an effect on the progeny (ROBERTSON and REEVE 1952 and later; TANTAWY 1959 on *Drosophila melanogaster;* PREVOSTI 1955 on *Drosophila subobscura*). Selection was effective in all cases, and minus selection shows more response than that in the plus direction.

In the present investigation the progeny of the selected females were measured for wing length and thorax length, and the results are reported in Table 6. Results

TABLE 6

Wing length in the selected offspring and the controls (sexes averaged) at different temperatures with their standard errors. Units of measurements are of 1/100 mm. Response to selection (sexes averaged) as percentage deviations from controls

		Controls	Offspring		Percent deviations from controls
Cage no.	Temperature	Wing (sexes avg.)	Size	Wing (sexes avg.)	
3	25°C.	199.81 ± 1.09	Large	200.64 ± 1.08	+ 0.42
			Small	198.47 ± 1.19	— 0.68
6	25°C.	199.73 ± 1.11	Large	200.17 ± 1.03	+ 0.22
			Small	198.99 ± 1.03	— 0.38
3	15°C.	226.16 ± 1.45	Large	226.80 ± 1.70	+ 0.28
			Small	225.16 ± 1.14	— 0.44
6	15°C.	229.05 ± 1.27	Large	229.86 ± 1.35	+ 0.36
			Small	227.14 ± 2.06	— 0.84

obtained for thorax length are not given since they show a similar behavior to wing length.

The results as presented in Table 6 indicate that the response to selection should be more pronounced if male parents were also selected. The results are presented most effectively as percentage deviations from controls. Response to selection in the minus direction is greater than that in the plus one, thus agreeing with the results of other investigators. The results also show that populations under their original temperature show almost the same response to selection. This may indicate that response to selection, measured as percentage deviations from controls, does not differ significantly from one population to another of the same species, provided they were selected under their original temperature conditions. Such results raise interesting questions which should be investigated, such as the effects of the original temperature conditions on natural populations of Drosophila.

CONCLUSIONS

The path coefficients analyses clearly indicate that body size in *Drosophila pseudoobscura* has definite effects on lifetime egg production. Such effects may differ according to the original temperature under which the populations have been kept for long time. TANTAWY and MALLAH (1961) found, in natural populations of *Drosophila melanogaster* and *D. simulans*, that the original climatic conditions have significant effects in determining various quantitative characters, and TANTAWY and VETUKHIV (1960) reported significant effects of temperature on egg laying capacity in populations of *Drosophila pseudoobscura.*

The present analyses indicate that egg production is a character which is influenced more by environmental conditions than by genetic agencies. ROBERTSON (1957) stated that nonadditive effects predominate in egg production in *Drosophila melanogaster*, while the situation is reversed in the inheritance of body size. Body size in *Drosophila pseudoobscura* behaves in the same manner as in *Drosophila melanogaster* and yields similar heritability estimates. The higher heritability estimates found in the present study indicate that selection in *Drosophila pseudoobscura* should be effective in increasing and decreasing body size.

Changes of the original temperature result in decline of the heritability estimates. This is expected on the basis that selection acts mainly on the additive genetic variance. Since heritability is defined as a ratio of the additive genetic variance to the total variation, it may be altered when either the numerator or the denominator is changed. Therefore, one may conclude that the decline in the heritability estimates in the present study is due to the increase of environmental variations as well as of the environment-genotype interaction, under the new conditions.

SUMMARY

1. An experiment was designed to study the effects of different temperatures and parental female sizes on the egg production rates in *Drosophila pseudoobscura*. Heritability of the body size and the response to selection in one generation were investigated.

2. The results show that temperature and body size affect the rate of egg production and the longevity. The path coefficient theory has been applied to the correlation coefficients between different characters.

3. The correlations between parental size and offspring size indicate that populations of *Drosophila pseudoobscura* possess a considerable amount of additive genetic variance for body size.

4. Changing the original temperature under which the populations have been maintained for a long time results in decline of the heritability estimates; this is followed by a decrease in the response to selection.

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DEVELOPMENTAL HOMEOSTASIS IN POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*

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DEVELOPMENTAL HOMEOSTASIS IN POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*[1]

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Among the chromosomes of *Drosophila pseudoobscura* the relative frequencies of the various gene arrangements vary with their geographical distribution. Dobzhansky (1943) reported that populations of *Drosophila pseudoobscura* which live in different habitats often differ in the relative frequencies of their inversions and that the composition of a population captured from one region may differ significantly from season to season, suggesting that in nature these karyotypes are subjected to natural selection. Similar results have been obtained by Dubinin and Tiniakov (1945) for *Drosophila funebris*.

These early findings indicate that the carriers of the various gene arrangements must possess different adaptive values in various environmental conditions. Such results have been confirmed in laboratory experiments in which populations of *Drosophila* were maintained artificially in cages under different environments. Thus, the data reported indicate that at colder or warmer temperatures populations carrying different gene arrangements do not reach equilibrium at the same frequencies. Wright and Dobzhansky (1946) and Dobzhansky (1947) have attributed such a situation to the fact that the heterozygous genotypes possess a higher adaptive value than either homozygous genotype.

After the pioneer work of Dobzhansky, many other investigators worked on the effects of several environmental conditions on quantitative traits in populations of *Drosophila* possessing various gene arrangements. For instance, Heuts (1948), Wallace (1948), da Cunha (1951), Levine (1952) and Moos (1955) working on populations of *Drosophila pseudoobscura*, Spiess and Schuellein (1956) and Spiess (1958) on populations of *Drosophila persimilis*, all agree that flies with various gene arrangements do not show the same adaptive values in different environments.

There is little evidence on the differences in component of fitness between the chromosomal types of Arrowhead (AR) and Chirichaua (CH) in populations of *Drosophila pseudoobscura* despite the extensive knowledge of the behavior of these chromosomal types in populations. The present experiments were designed to investigate the adaptive values of the two homozygous populations as well as the F_1's generation maintained under different environmental conditions. Some other crosses were carried out to study the facilitation, if any, among the various arrangements of gene combinations.

TECHNICAL PROCEDURES

Two populations of *Drosophila pseudoobscrua* homozygous for the Arrowhead and Chirichaua gene arrangements in the third chromosome kept for two years in population cages were used as basis of the present experiments. The foundation stocks were prepared by using sixteen strains homozygous for AR, and thirteen strains homozygous for CH, all derived from flies collected in the locality of Pinon Flats, Mount San Jacinto in California. For more details concerning the maintenance of these populations, i.e., No. 180 for AR and 182 for CH, and crossing for population cages, see Beardmore, Dobzhansky, and Pavlovsky (1960). All populations were kept in wooden cages at 25° C from which samples used for the present experiments were taken. At the begin-

[1] The present work was carried out during the author's tenure of the Boese Fellowship at the Department of Zoology, Columbia University, New York, N. Y., U. S. A.

ning of the experiments, cups were taken from each cage to separate virgin females of both homozygous classes and then crosses were made within and between populations. These parental crosses were maintained at temperatures similar to that of the original cages. After hatching, virgin females of AR/AR, CH/CH, and AR/CH were separated from males. Crosses within and between the first two groups were carried out to obtain the parental and the first generations. Females and males of AR/CH were crossed to obtain the second generation and heterozygous females were also backcrossed with AR/AR and CH/CH males. These six different crosses were designated as P_1, P_2, F_1, F_2, $B_{F_1P_1}$, and $B_{F_1P_2}$, respectively.

Four different temperatures, i.e., 15° C, 25° C, 27°C and a fluctuating one (designated F° C), were used. For the fluctuating temperature, populations were kept for twenty-four hour periods at 15° C, 25° C, and 27° C in succession.

Lifetime egg production: Females of AR/AR, CH/CH, and AR/CH genotypes were used to estimate the lifetime egg production at the four different temperatures. At each temperature, ninety virgin females of each genotype were taken at random and crossed with the same number of males of appropriate genotypes for other parts of the experiment. Thus, the total number of females used in the present experiment was 1,080.

At each temperature, ten females and ten males were kept in separate vials. Each vial contained a paper spoon with the usual cream-of-wheat-molasses medium with a drop of Fleischmann's yeast. Every day spoons from the total of 108 vials were removed from the vials and were replaced with new spoons holding fresh food and yeast. Eggs were counted on each spoon under a binocular microscope. To avoid crowding, spoons were changed and counted twice a day at twelve-hour intervals for the first six weeks, after which counts were made daily. Such a procedure allowed us to count eggs with great accuracy and without injuring the eggs. At the time of changing spoons, dead females were counted and discarded and the death date was recorded.

Percentage of emergence: For each of the six crosses daily egg output for only twenty females were put in food bottles. To avoid crowding in bottles, eggs were counted and cultured twice a day for the first six weeks. After hatching adults were counted and classified as to sex. Such counting of adult flies took place initially at the end of the first two days of emergence and then once every four days thereafter for warmer temperatures and once a week for the colder ones.

Body size and body weight: For each cross parents were allowed to lay eggs at 15° C, 25° C, and 27° C, i.e., crosses were kept for 24 hours under each temperature and then moved to the next temperature. Following the 27° C period the parents were returned to 15° C and the sequence was repeated four times, so that eggs from five days at each temperature were collected. Eggs were cultured, not more than 100 eggs, in each food bottle. Adults after hatching were collected and kept in fresh food bottles for the measurements of body size, i.e., wing and thorax length. Body size was measured by the method recommended by Robertson and Reeve (1952a), and used by the author previously (Tantawy, 1959).

For body weight, a microchemical 100-A Quartz Helix balance was used with which individual flies can be weighed. Flies used for body weight were kept in empty vials for eight hours after hatching and then weighed immediately. Five males and five females from each bottle for each cross were measured on each of the five days giving a total of 25 males and 25 females from each cross.

Longevity: The different crosses were maintained under each of the four temperatures, and the hatched offspring used for studying longevity. From each cross at each temperature 500 pairs of males and females were used with 50 pairs being kept per food bottle. All the flies used in this study were collected within a period of 24 hours. At 15° C the surviving adults in each bottle were transferred at weekly intervals to fresh food bottles and the number of deaths (fe-

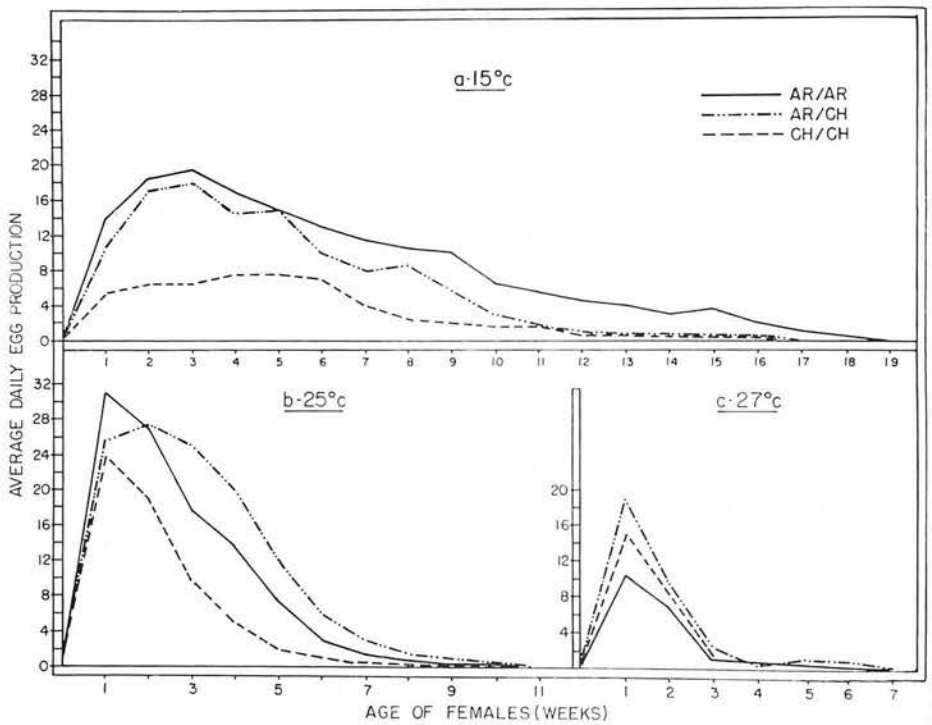

FIG. 1. Daily lifetime egg production for females of different gene arrangements at various temperatures. Each point represents the daily average in a given week.

males only) occurring during the week was determined by counting the dead flies. For warmer and fluctuating temperatures flies were transferred twice a week.

RESULTS AND DISCUSSION

Lifetime Egg Production

The relationship between lifetime egg production for females of different gene arrangements maintained at 15°C, 25°C, and 27° C are presented in figure 1. The results are reported as averages per day per female in a given week. The average daily egg production increases rapidly to the end of the first week of age in females maintained at the warmer temperatures, and more slowly at the colder one. At 25°C and 27° C the highest peaks for all genotypes are at about the end of the first week, whereas the peak appears at the end of the third week of age at 15° C. Such peaks are uniform for females with different gene arrangements (with significant differences) kept at the same temperature.

Comparing the effects of the different genotypes on egg-laying capacity, it may be seen that females of AR/AR reared at 15° C are superior to those of CH/CH, while those of AR/CH are intermediate. At 25°C the AR/CH females (apart from the first week) are superior to all other genotypes while females of AR/AR are intermediate. At both temperatures, the CH/CH females lay the fewest eggs. The situation at 27° C is different, with AR/CH females superior and AR/AR females inferior to CH/CH females.

Figure 2 reports the total lifetime egg production of the same number of females (90 females in each group) at the four different temperatures. The results show clearly significant effects of temperature on egg production which agree well with those found by Tantawy and Vetukhiv (1960) working on populations of *Drosophila pseudoob-*

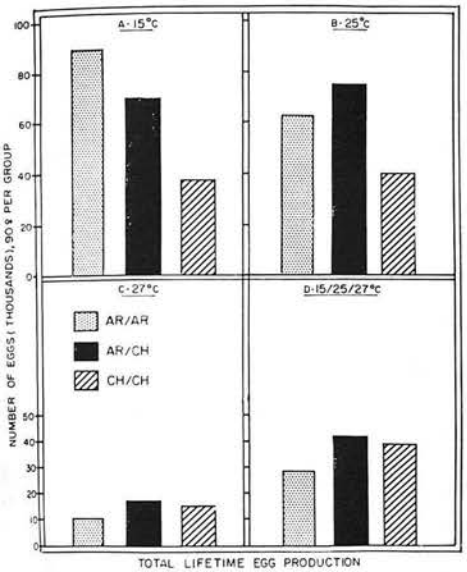

FIG. 2. Total oviposition rate for females of different genotypes at different temperatures (90 females in each group). Probabilities (based on the average lifetime per female) between:

(AR/AR–CH/CH) $<$ 0.001 at 15° C and 25° C, $<$ 0.5 at 27° C, and $<$ 0.2 at F° C.

(AR/AR–AR/CH) $<$ 0.001 at 15° C, $<$ 0.01 at 25° C and F°C, and $<$ 0.3 at 27° C.

(CH/CH–AR/CH) $<$ 0.001 at 15° C and 25° C, $<$ 0.7 at 27° C and $<$ 0.3 at F° C.

scura. The results also illustrate significant differences in egg-laying capacity between females with various gene arrangements. Tests of significance between different genotypes are presented in the caption of figure 2.

The most important feature of figure 2 is the results obtained from the fluctuating temperature. Under such temperature conditions differences in egg production between genotypes are similar to those obtained at 27° C, but the total number of eggs is intermediate between the numbers obtained at 25° C and 27° C.

The results as reported in figures 1 and 2 indicate clearly that different gene arrangements possess various adaptive temperature norms. These results will be discussed later. Similar findings have been reported earlier by Wallace (1948) who showed, in the same species, that at 25° C the SR/ST gene arrangement is superior in fecundity to the two homozygous groups and SR/SR is superior to ST/ST, but that at 16.5° C, the latter is superior to the former. Heuts (1948), Levine (1952), and Moos (1955) reported similar physiological behavior. Da Cunha (1951) obtained similar results when studying the effects of different nutritional conditions in the same species.

Percentage of Emergence and Sex-Ratio

Viability is measured as the percentage of emergence of adults from a given number of eggs cultured in ordinary food bottles. Table 1(a) reports the total lifetime egg production for twenty females in each group at each temperature and the percentage of emergence, as well as the sex-ratio. Table 1(b) shows tests of significance for percentage of emergence between different genotypes.

The results as given in table 1(a) indicate clearly significant differences between temperatures. Eggs obtained from the crosses of both homozygous groups show the highest viability at any given temperature. At 15° C and 25° C crosses within AR/AR show greater viability than those within CH/CH. But at 27° C and F° C, the latter genotype is superior to the former.

Percentage of emergence from eggs to adults is higher for the F_1 generation than for the F_2's, the differences being significant at 15° C and 25° C but not at 27° C and F° C. Females of the F_1, backcrossed to AR/AR males, show greater viability (though not significantly so) than the backcrosses to CH/CH males at 15° C and 25° C. At the other two temperatures the situation is reversed.

Sex-ratio data, as shown in table 1a(C), indicate that at 15°C and 25° C the number of females is greater though not significantly so. At 27° C and F° C there are significant differences between sexes (the level of significance is 1%) with females in excess. These results indicate that females resist changes in temperatures more, and are bet-

TABLE 1a. *Number of eggs cultured (A), percentage of emergence (B), and sex-ratio (C). See text for designation of crosses*

	Crosses	15° C			25° C			27° C			F° C		
		A	B	C	A	B	C	A	B	C	A	B	C
(1)	P_1	37108	76.41	53.81	16786	59.05	53.29	2711	7.52	63.03	7624	43.88	61.01
(2)	P_2	6797	66.64	53.37	7849	52.06	57.75	5085	10.36	65.31	5693	54.61	62.45
(3)	F_1	12897	82.63	51.89	11400	66.26	54.80	3487	15.11	68.06	7202	56.11	63.15
(4)	F_2	10932	77.46	53.62	21837	56.56	56.69	3785	14.82	66.26	10834	49.27	62.21
(5)	$B_{F_1P_1}$	11983	78.67	52.96	11707	61.93	51.70	2816	12.11	64.25	4996	53.62	59.84
(6)	$B_{F_1P_2}$	7134	77.17	52.55	7040	61.72	53.20	2130	14.32	66.41	9093	56.00	57.67

b. *Probabilities for percentage of emergence (B) (based on weekly averages) between:*

Crosses	15° C						25° C						27° C						F° C					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
1		*	*	–	–	–		*	*	–	–	–		–	*	*	*	*		*	*	–	*	*
2			**	**	**	**			**	*	**	**			*	*	–	*			–	*	–	–
3				*	–	*				**	–	–					–	–	–				*	–	–
4					–	–					*	*					–	–					*	*
5						–						–						–						–

* Significant at the level of 5%.
** Significant at the level of 1%.
– Insignificant.

TABLE 2. *Variance (σ^2) of logarithms of measurements for wing length, thorax length, and body weight at various temperatures. See text for designation of crosses*

Crosses	15° C		25° C		27° C	
	Males	Females	Males	Females	Males	Females
a. *Wing length*						
P_1	0.000085	0.001040	0.000067	0.000104	0.000456	0.000478
P_2	0.000314	0.000232	0.000117	0.000123	0.000332	0.000296
F_1	0.000173	0.000181	0.000109	0.000105	0.000213	0.000275
F_2	0.000364	0.000235	0.000313	0.000324	0.000378	0.000567
$B_{F_1P_1}$	0.000111	0.000205	0.000205	0.000211	0.000389	0.000453
$B_{F_1P_2}$	0.000346	0.000231	0.000318	0.000400	0.000299	0.000314
b. *Thorax length*						
P_1	0.000123	0.000215	0.000150	0.000158	0.000415	0.000462
P_2	0.000305	0.000413	0.000279	0.000341	0.000311	0.000450
F_1	0.000261	0.000197	0.000234	0.000199	0.000247	0.000234
F_2	0.000433	0.000497	0.000316	0.000405	0.000497	0.000489
$B_{F_1P_1}$	0.000364	0.000376	0.000560	0.000489	0.000539	0.001059
$B_{F_1P_2}$	0.000418	0.000395	0.000617	0.000598	0.000437	0.000493
c. *Body weight*						
P_1	0.001985	0.002531	0.000813	0.001211	0.001933	0.001598
P_2	0.002633	0.003631	0.001825	0.002031	0.001845	0.001936
F_1	0.001409	0.001788	0.001101	0.001012	0.001198	0.001937
F_2	0.002631	0.003617	0.002351	0.002616	0.001873	0.002137
$B_{F_1P_1}$	0.001636	0.002113	0.001131	0.001545	0.002714	0.002596
$B_{F_1P_2}$	0.001907	0.002231	0.001725	0.001845	0.002235	0.002411

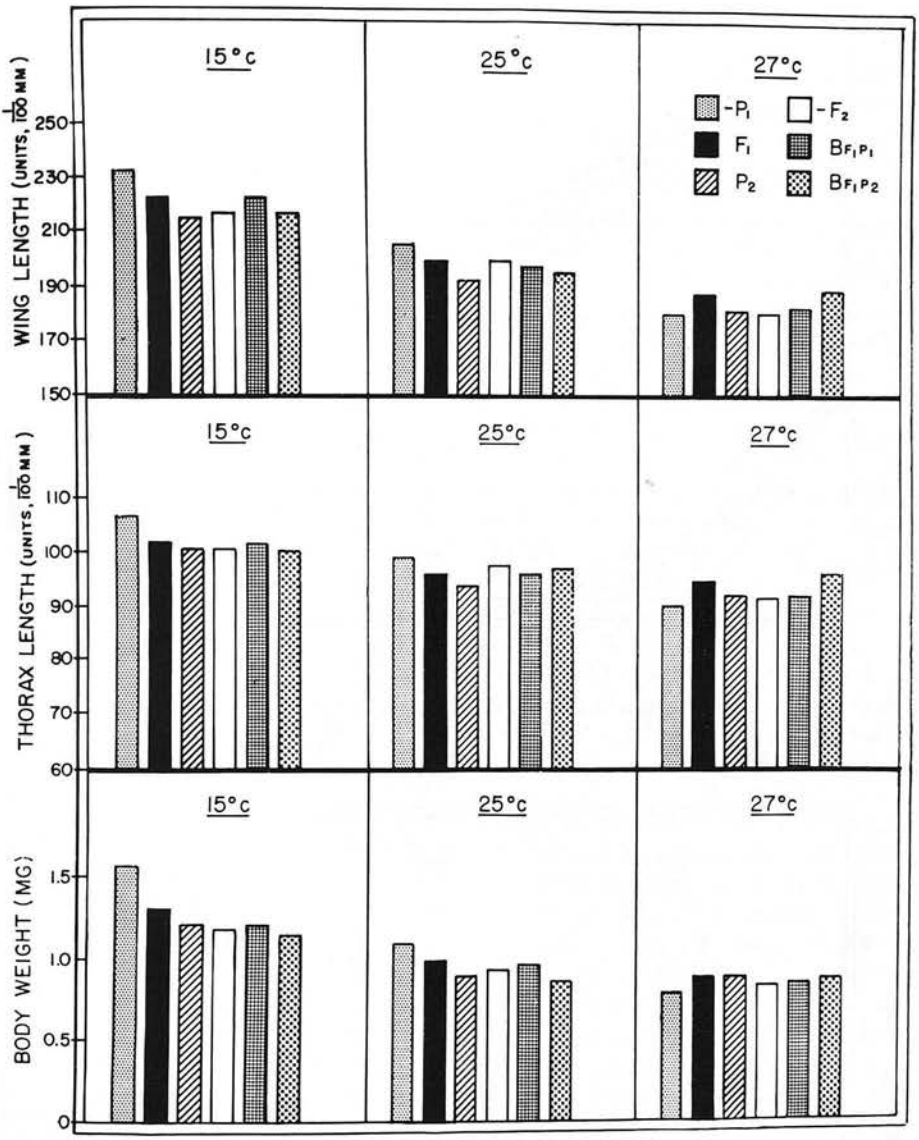

FIG. 3. Average measurements and weights (sexes averaged) for wing and thorax length 1/100 mm and body weight in mg for flies of different gene arrangements at various temperatures.

ter buffered than males. The same conclusions have been reached by Tantawy and Mallah (1961) who worked on natural populations of *D. melanogaster* and *D. simulans*.

Body Size and Body Weight

Body size, i.e., wing and thorax length, and body weight of the offspring resulting from the six different crosses are shown in figure 3, and the variance (σ^2) of logarithms of measurements are given in table 2. Logarithms have been used here to cancel out the effect of the absolute size on variance, since these are often correlated.

The results indicate highly significant differences between temperatures. The flies are much larger and heavier at colder temperatures than at warmer ones. Tantawy

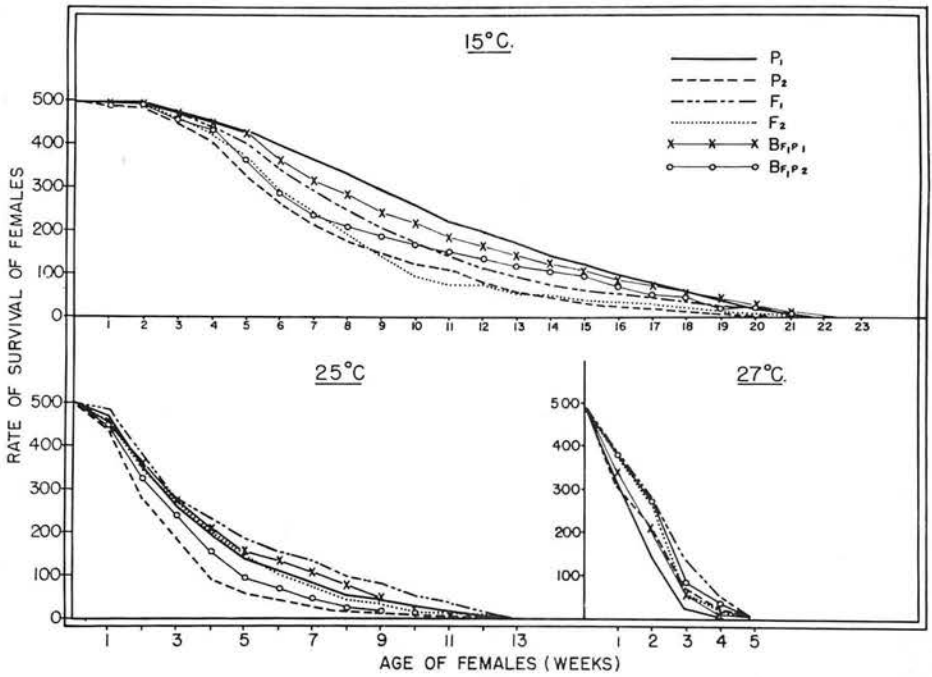

FIG. 4. Rate of survival of females of different genotypes.

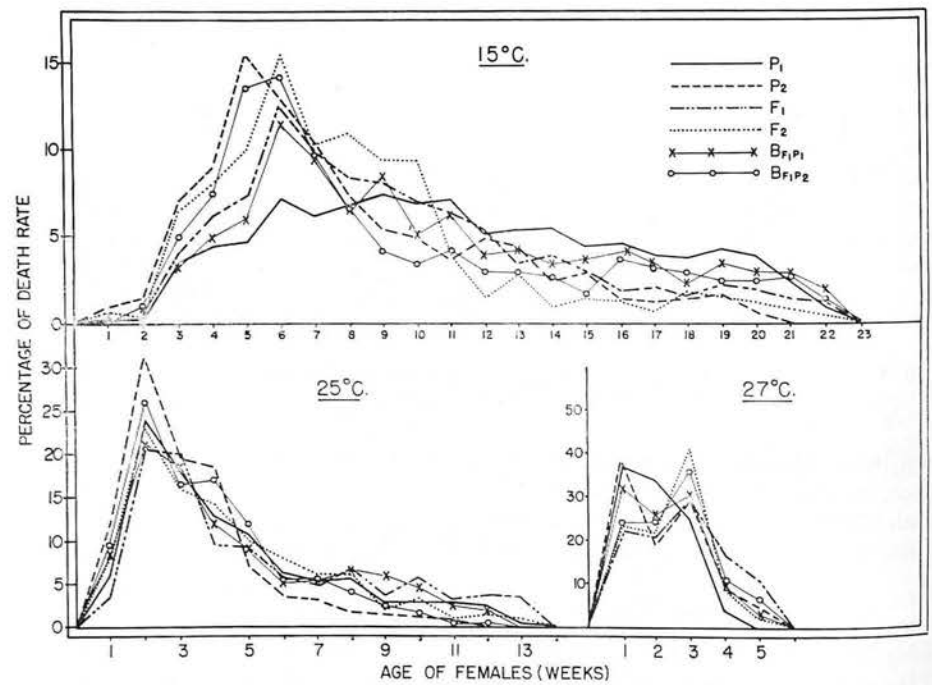

FIG. 5. Percentage of death rate in females of different genotypes.

and Mallah (1961) and Robertson (1959) reported significant effects of temperature on wing length. Robertson (1959) attributed such an increase at colder temperature "Almost entirely to a change in cell size." He also concluded that "cell number remains comparatively constant." The present results also indicate significant positive correlations between body size and body weight.

Comparing the different crosses at various temperatures, it is apparent that the offspring within the homozygous AR/AR have longer wing and thorax length with heavier body weight for both sexes at 15° C and 25° C. Crosses between the two homozygous groups produce larger offspring at 27° C, while those within the CH/CH genotype have larger offspring than those within the AR/AR group at 27° C. The excess of the F_1 generation over the mid-parent will be considered in a later section. The results also indicate a tendency for a phenotypic correlation of body size and body weight with reproductive rate, as measured by egg production.

Measurements of both characters for the F_1 generation exceed those for the F_2. The backcrosses are generally intermediate between the F_1 and the recurrent parent.

Examination of the variance (σ^2) of the logarithms of measurements (table 2) shows significant differences between temperatures. Within temperatures significant differences also occur between genotypes. At 15° C and 25° C the CH/CH genotype is more variable than AR/AR (significant at the 5% level). In all characters studied the F_1 generation is generally (but not always) less variable than parents, while the F_2 shows insignificantly higher variability than the parental generations. Offspring resulting from backcrossing F_1 females with AR/AR males at 15° C and 25° C are less variable than those obtained from CH/CH males (the differences being significant at the 5% level). The situation at 27° C is reversed in favor of CH/CH genotype.

Longevity

The longevity of adult females resulting from different crosses is shown in figures 4 and 5, respectively, as the number of surviving females and as death rate. The results in figure 4 indicate that at 15° C AR/AR females are superior to AR/CH, which in turn are superior to all other females except for $B_{F_1P_1}$. At 27° C CH/CH females live longer than AR/AR females. The F° C group (not shown) show values intermediate between those obtained at 25° C and 27° C.

Figure 5 shows that at 15° C the highest values for death rate are different for different genotypes. Peaks are found at the end of the fifth week in CH/CH females and at the sixth week of age in other groups. At 25° C the highest peak is found at the end of the second week of age in all groups. The results at 27° C, where two peaks can be found in all groups, are unexpected. They could be accounted for by some undetectable unfavorable environmental conditions occurring at the end of the third week of age.

Table 3a shows the average longevity (days) for females in the fecundity and the longevity experiments. The results indicate that females of the latter experiment live longer than those of the former. This could be due to "laboratory error." Table 3a (A, B) indicates that at 15° C the longevity of F_1 females is intermediate between those of the parents, while at the other temperatures it is higher. There is a decline (table 3a(B)) in the F_2 longevity compared with that of the F_1. At 15° C and 25° C offspring of AR/CH females backcrossed to AR/AR males live longer than those from the CH/CH backcross, while at 27° C and F° C the situation is reversed. Tests of significance (table 3b) indicate that significant differences exist between most of the longevity means at 15° C and 25° C but not at 27° C.

Conclusions

It is well known from population cage experiments with *Drosophila pseudoobscura* (Wright and Dobzhansky, 1946; and Dob-

TABLE 3a. *Average longevity (days) for females used in fecundity experiment and longevity experiment with their standard errors. See text for designation of crosses*

Crosses		15° C	25° C	27° C	F° C
A. *Fecundity experiment*					
(1)	P_1	74.18 ± 3.52	30.55 ± 3.01	11.60 ± 4.91	19.61 ± 3.81
(2)	P_2	49.93 ± 5.13	21.26 ± 4.62	14.93 ± 3.79	24.64 ± 2.91
(3)	F_1	63.92 ± 3.92	33.71 ± 2.32	16.23 ± 4.22	29.23 ± 1.38
B. *Longevity experiment*					
(4)	P_1	79.80 ± 3.01	31.46 ± 2.50	13.72 ± 4.11	20.01 ± 3.15
(5)	P_2	56.04 ± 4.21	23.24 ± 3.56	15.62 ± 4.23	26.40 ± 3.49
(6)	F_1	66.53 ± 2.34	36.85 ± 2.49	19.12 ± 3.93	30.22 ± 2.93
(7)	F_2	57.53 ± 4.39	30.73 ± 3.82	17.09 ± 4.41	24.00 ± 3.92
(8)	$B_{F_1P_1}$	74.07 ± 3.52	32.62 ± 3.44	15.68 ± 3.81	26.21 ± 3.76
(9)	$B_{F_1P_2}$	66.12 ± 4.94	27.09 ± 4.01	17.85 ± 3.34	28.05 ± 7.80

zhansky, 1948) that inversions confer different adaptive values on their carriers. Moreover, these differences in adaptive value are sensitive to temperature. Briefly, no differences in adaptive value can be observed at 15° C, while at 25° C the order of adaptive values is AR/CH>AR/AR> CH/CH. The results of the present experiments show that the components of fitness —fecundity, longevity, and viability—can in large part explain the population cage observations. In table 4 the relative fitness values of the various crosses for the different components of adaptive value are listed. The heterozygotes are arbitrarily assigned the fitness 1.000. As the table shows, the order of fitness values at 25° C is AR/CH> AR/AR>CH/CH for all components of the life cycle. At the even higher temperature of 27° C and at F°C there is still heterosis, but the fitness of the two homozygotes is reversed, i.e., AR/CH>CH/CH>AR/AR. It would be extremely informative to maintain population cages under fluctuating conditions to see whether the equilibrium frequencies of the inversion correspond to the fitness components as they do at 25° C. At 15° C the results are equivocal, with heterosis shown for viability, but not for the other fitness components. This also agrees with the population cage results, although the consistent inferiority of CH/CH at 15° C does not.

A point of considerable interest is the sim-

TABLE 3b. *Significance levels for differences in longevity: (longevity experiment). The values shown refer to % level of significance. Minus signs indicate lack of significance*

Crosses	15° C						25° C						27° C						F° C					
	4	5	6	7	8	9	4	5	6	7	8	9	4	5	6	7	8	9	4	5	6	7	8	9
4		6	5	5	8	7		7	8	–	–	8		–	8	–	–	8		8	8	–	8	8
5			7	–	6	8			6	8	7	–			–	–	–	–			8	–	–	–
6				7	7	–				8	8	7				–	–	–				8	8	–
7					8	8					–	–					–	–					–	–
8						8						8						–						–

(fecundity experiment)

Crosses	15° C			25° C			27° C			F° C		
	1	2	3	1	2	3	1	2	3	1	2	3
1		5	7		8	8		–	–		8	6
2			7			6			–			8

TABLE 4. *The relative fitness for flies of different gene arrangements at various temperatures*

Temperature	P_1	F_1	P_2	P_1	F_1	P_2
a. *Egg production*				c. *Longevity (fecundity experiment)*		
15° C	1.400	1.000	0.525	1.161	1.000	0.781
25° C	0.828	1.000	0.525	0.906	1.000	0.631
27° C	0.616	1.000	0.857	0.715	1.000	0.920
F° C	0.702	1.000	0.834	0.671	1.000	0.843
b. *Percentage of emergence*				(*longevity experiment*)		
15° C	0.925	1.000	0.807	1.199	1.000	0.842
25° C	0.891	1.000	0.786	0.854	1.000	0.631
27° C	0.498	1.000	0.686	0.718	1.000	0.817
F° C	0.782	1.000	0.973	0.662	1.000	0.874

ilarity of the results from the 27° C and the F° C experiments. It appears that in a fluctuating environment of high periodicity, it is the extreme high temperature that is most influential in determining results. The similarity exists not only for the fitness components but for the metric characters as well. It should be pointed out, however, that these results are at variance with those obtained by Vetukhiv and Beardmore (1959) in their experiments on crosses between geographical populations. In their work, the results under fluctuating temperature, if anything, more closely resembled those obtained under the lower temperature.

The second point of importance that can be derived from our experiments is the relation between variability and fitness. Considering variability between replicates and between individuals within temperatures, it is generally clear that greater fitness is associated with lower variability (tables 3a and 4). The superior genotype at any given temperature produces less phenotypic variability both for fitness components and for metric characters. The picture is not the same, however, when variability between temperatures is considered. For longevity (fecundity experiment) table 3a(A), the coefficient of variation of the genotypes AR/CH, AR/AR, and CH/CH are 0.517, 0.741, and 0.349, respectively. That is, the poorest genotype has the lowest coefficient of variability between temperatures. For longevity (longevity experiment), table 3a(B), the corresponding values are 0.531, 0.826, and 0.585. In this case the poorest genotype and the best show roughly equal coefficients of variability, while AR/AR individuals, whose mean longevity is not very much different from the AR/CH (36.25 days as opposed to 38.18 days), have the highest coefficient of variability. It is clear, then, that great care must be exercised in the interpretation of variability as an index of buffering.

Phenotypic variation may be caused by genetic diversity, environmental agencies, and interaction of both. Many results have been obtained to show that in populations of *Drosophila* adaptation to environment depends on a heterozygous genotype. Thus, Robertson and Reeve (1952a) and Mather (1953), and Smith and Smith (1954) have reported that, when exposed to the same variety of environmental stimuli, heterozygotes produce more uniform phenotypes than do homozygotes. The development of the heterozygotes is then on the average better buffered against environmental disturbances than that of homozygotes. Dobzhansky and Wallace (1953) considered this phenomenon to indicate a superior homeostatic adjustment of the developmental pattern in an average heterozygote. Robertson and Reeve (1952b) suggested that the decrease of the variance following hybridization may be due to greater biochemical versatility of the heterozygotes. Lewis (1954) supported the idea that biochemical versatility would be manifest, at least in part, in alternative pathways of biosynthesis functional under different environmental optima. Lerner (1954) argued that "heterozygosity has a dual function in the life of Mendelian populations. On the one hand, it provides a mechanism for maintaining genetic reserves and potential plasticity, and on the other, it permits a large proportion of individuals to exhibit combinations of phenotypic properties near the optimum. Underlying both processes is the superior buffering ability of heterozygotes with homozygotes."

TABLE 5. *Percentage of heterosis in different characters manifested at various degrees of temperature*

Character	15° C		25° C		27° C		F° C	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Egg production	3.9±1.4	—	4.8±5.6	—	35.8±4.4	—	30.2±3.9	—
Percentage of emergence	11.1±3.1	5.9±2.3	10.7±2.4	1.0±3.1	6.2±3.3	5.9±4.1	6.8±4.2	−0.1±1.4
Wing length	−0.9±0.5	−1.9±0.4	0.3±0.2	0.5±0.2	3.6±0.5	0.1±0.2	—	—
Thorax length	−2.5±0.4	−3.2±0.6	−0.5±0.4	0.9±0.5	3.7±0.3	0.7±0.4	—	—
Body weight	−8.6±2.1	−16.4±4.3	−2.0±2.4	−7.0±4.5	4.7±3.4	5.9±2.6	—	—
Longevity:								
Fecundity exp.	3.0±1.1	—	30.2±5.6	—	22.4±6.4	—	32.1±5.8	—
Longevity exp.	−2.0±2.3	−15.3±7.4	34.4±5.5	12.4±6.7	30.3±5.6	16.5±7.3	30.3±4.9	3.5±3.4

One may conclude from the above discussion that a population possesses greater adaptation than another population if it is adapted to a greater variety of environments (Lewontin, 1957). Therefore, the AR/CH heterozygotes may be viewed as being better buffered against environmental disturbances, i.e., more homeostatic, since they can live longer and produce more offspring than any other populations in a wide variety of environments. A similar test of this phenomenon was made by Dobzhansky and Levine (1955) using a range of temperature and food sources in *Drosophila pseudoobscura*. They reported that homozygotes have a low average fitness and a high variability as compared with heterozygotes.

Two explanations have been advanced to account for superior homeostasis in heterozygous individuals. The first attributes it to versatility in development of heterozygotes beyond that found in homozygotes. The second view sees no special properties in the heterozygosity except the classic one of promoting segregation, which leads to superior buffering in hybrids by virtue of the heterozygous balance achieved in outbreeding species by natural selection.

Percentage of heterosis may be expressed as the ratio of the F_1 or F_2 means to the average value for the parents (Tantawy, 1957). The results are presented in this form in table 5 which includes all characters studied at the different temperatures. The general conclusions which can be drawn from such results are that the F_1 hybrids show a heterotic increase for egg production, percentage of emergence, and longevity, over the parental level, and that the F_2 generation shows a breakdown of heterosis. Body size and body weight display negative heterosis at 15°C, and positive heterosis at 27° C. In the intermediate temperature the direction of heterosis is variable.

The results of table 5 indicate clearly that even when heterosis is present in F_1 hybrids it is not necessarily found in all characters. They are in agreement with those reported by Vetukhiv and Beardmore (1959). Another point of interest is that heterosis for most of the characters is strongest in populations reared at 27° C. It has been suggested by Lerner (1954) that euheterosis is connected with developmental homeostasis. From the results previously reported, one may gather that 27° C is the most stringent environment for populations of *Drosophila pseudoobscura*. Therefore, one expects that heterosis is likely to be more manifested at the 27° C than at other temperatures. This is in agreement with Wallace (1948), who measured many physiological traits in the life cycle of "Sex-ratio" and "Standard" genotypes of *D. pseudoobscura*. He reported that females heterozygous for ST/SR chromosomes showed heterosis more strongly at high than at low temperatures. Moriwaki, Ohnishi, and Nakajima (1956), who investigated the comparative viability of gene arrangement homozygotes and heterozygotes in *D. ananassae*, demonstrated that no heterosis was found under optimal conditions but was observed under unfavorable ones.

Summary

1. Laboratory populations of *Drosophila pseudoobscura* carrying AR/AR and CH/CH gene arrangements were the basis of the present experiments. Various crosses were made to study the productive capacity measured as lifetime egg production, percentage of emergence, body size, i.e., wing and thorax length, body weight and longevity of adult females. Four different experimental treatments were used: constant temperatures of 15° C, 25° C, 27° C, and a fluctuating one between these three.

2. Lifetime egg production differed significantly between temperatures: 15° C gave the highest egg production while 27° C gave the lowest. AR/AR was found to be the best genotype at 15° C while AR/CH is superior at 25° C, 27° C and at the fluctuating temperature. CH/CH is generally inferior to all types except that at the warmer temperatures; it is superior to AR/AR.

3. Percentage of emergence, body size, body weight and longevity give substantially the same picture as that found for egg production.

4. Variances of quantitative characters of the superior gene arrangements at a given temperature are often smaller than of the poorer ones.

5. The relative indexes of fitness show that the heterozygous genotypes are the most adapted ones, while the CH/CH is the least.

6. The F_1 hybrids generally show heterosis in egg production, viability, and longevity. Body size and body weight display more heterosis at 27° C than at 15° C or 25° C. In the F_2 generation a breakdown of heterosis occurs in all the characters studied.

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DEVELOPMENTAL HOMEOSTASIS IN X-RAYED POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA* [1])

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An experiment was designed to study the effects of various dosages of X-ray irradiation on different gene-arrangements (AR and CH) of the third chromosome of *D. pseudoobscura*, with respect to quantitative characters.

Egg production showed an insignificant decline at 1500r and an increasingly strong reduction by 3000 and 4500r. Other characters studied (emergence, longevity, body size and weight) generally showed the same trend.

Irradiation of both gene-arrangements usually gave more reduction in fitness characters than did irradiation of one gene arrangement alone. Irradiation caused an increase in phenotypic variability as expressed by coefficients of variation.

Heterosis in F_1 was observed for most of the characters studied, and a breakdown of heterosis in F_2. Heterosis was enhanced by irradiation at higher dosages.

Relative indices of general performance indicate that the adaptive values decreased with the increase in radiation dosages. In all cases the heterozygous genotypes are the fittest while the CH/CH homozygote was the least fit.

Introduction

It is a well known fact that the use of X-irradiation has widespread deleterious effects on the offspring in the subsequent generations. The biological action of radiation is most plausibly attributed to chemical changes from ionization. The genetic effects are due mainly to point mutations arising by radiation which confer harmful effects on individuals carrying them. In the case of recessive lethal mutations induced by irradiation of *Drosophila melanogaster* spermatozoa, it has been demonstrated that the relation between frequency and dose is substantially linear over a very wide range.

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The effects of different doses of X-irradiation on quantitative characters in laboratory animals have been investigated by various workers. Thus, GOWEN & STADLER (1952), HERSKOWITZ & ABRAHAMSON (1956), ABRAHAMSON & HERSKOWITZ (1957) and others have shown a linear decline in egg production in *D. melanogaster* as dosage of radiation increases. HERSKOWITZ (1957) and others reported that X-irradiation in *D. melanogaster* females causes a significant increase in egg mortality. Shortening of lifespan was noticed by BAXTER & TUTTLE (1957) in *Drosophila*, by CORK (1957) in the flour beetle, by WHARTON & WHARTON (1959) in the cockroach, and by ALEXANDER & CONNEL (1960) in mice. Reduction in fertility was demonstrated by KING (1952) in *D. melanogaster*, by YANDERS (1954) in *D. robusta*, and by PARK, DE BRUYN & BOND (1958) in the flour beetle. WALLACE & KING (1951) reported that irradiation caused a decline in the fitness of *D. melanogaster*.

The present experiments were undertaken to investigate the genetic effects of various doses of X-irradiation in progeny carrying a descendant of one or two irradiated third chromosomes, one of the largest autosomes in *D. pseudoobscura*. Other chromosomes could not be controlled and were disregarded. Some quantitative characters, i.e. lifetime egg production, percentage of emergence from egg to adult stage, longevity, body size, i.e. wing and thorax length and body weight in populations of *D. pseudoobscura* possessing different gene arrangements, i.e. Arrowhead (AR) and Chiricahua (CH) of the third chromosome, were under observation. For references concerning the experimental work on various gene arrangements in *Drosophila*, see TANTAWY (1961). The manifestation of heterosis in the first generation and possible breakdown in the second one was of particular interest. Crosses, other than F_1 and F_2 generations, were carried out to provide complete data for comparison with those obtained previously (TANTAWY, 1961) in which the same populations were used but subjected to various temperatures.

Technical procedure

Two populations of *D. pseudoobscura* homozygous for the Arrowhead (AR/AR) and Chiricahua (CH/CH) gene arrangements of the third chromosome and kept for three years in population cages were used as the basis of the present experiments. The same populations were

used by the author (TANTAWY, 1961) in a study of the effects of four different temperatures on the same quantitative characters studied here. Details of the origin of these populations and of the crosses required for their maintenance are contained in the earlier paper.

Virgin males of AR/AR and CH/CH were given different doses of X-irradiation, i.e. 0 r, 1500 r, 3000 r and 4500 r. Radiation was delivered from a G.E., S.R.T. beryllium window machine using the following factors: 100 KVP, 6 ma, added filtration of 1 mm. al., target distance of 15 cm., and a dose rate of 100 r/minute (air). During the treatments the flies were kept in small gelatine capsules (50 males in each) on a petri dish. Temperature at the time of irradiation was about 25°C.

After irradiating the males, crosses with virgin females of *Bl Sc/L* stock were carried out, using the following procedure, e.g. for AR/AR males. P: ♀♀ *Bl Sc/L* × ♂♂ AR/AR. F_1: ♀♀ *Bl Sc/L* × ♂♂ AR/*Bl Sc*. F_2: ♀♀ *Bl Sc/L* × ♂♂ AR/*L*. The underlined gene arrangements AR or CH as the case may be, indicate origin from an irradiated ancestor. The technique was essentially the same for all doses and genotypes. Male offspring appearing in the F_2 generation, i.e. AR/*Bl Sc* or CH/*Bl Sc*, in the different dosage groups were used for crosses with virgin females of known genetic background, i.e. AR/AR and CH/CH to obtain the desired females for the egg production experiment and for other crosses. The females used for measuring egg laying capacity were: AR/AR, CH/CH, AR/CH, AR/CH, AR/AR, AR/CH and CH/CH. The last three irradiated genotypes were obtained by crossing AR/*Bl Sc* and CH/*Bl Sc* within and between populations. At the same time virgin females of AR/AR, CH/CH and AR/CH from the control populations were obtained.

After obtaining the required number of females for the egg production experiment, various crosses were carried out. Table 1 illustrates the control crosses and some of the 48 "irradiated" crosses which were maintained for each dosage of irradiation. Offspring resulting from crosses No. 8–17, No. 18–36, No. 37–48 and No. 49–55 should possess 25%, 50%, 75% and 100% irradiated third chromosomes, respectively. Such crosses were made for each different dosage to obtain the parental, first, second generations and both backcross generations (Table 1) which were designated as P_1, P_2, F_1, F_2, B_{F1P1}, and B_{F1P2}, respectively. For more details concerning such crosses the

TABLE 1

TYPE OF CROSSES CARRIED OUT BETWEEN MALES AND FEMALES CARRYING DIFFERENT IRRADIATED GENE-ARRANGEMENTS ON THE THIRD CHROMOSOME

Cross No.	Generation	♀♀	♂♂	Cross No.	Generation	♀♀	♂♂
Controls				15	B_{F1P1}	AR/CH	AR/AR
1	P_1	AR/AR	AR/AR	16	B_{F1P2}	AR/CH	CH/CH
2	P_2	CH/CH	CH/CH	17	B_{F1P1}	AR/CH	CH/CH
3	F_1	CH/CH	AR/AR				
4	F_1	AR/AR	CH/CH	18	P_1	AR/AR	AR/AR
5	F_2	AR/CH	AR/CH	..			
6	B_{F1P1}	AR/CH	AR/AR	34	B_{F1P2}	AR/CH	CH/CH
7	B_{F1P2}	AR/CH	CH/CH	35	B_{F1P2}	AR/CH	CH/CH
				36	B_{F1P2}	AR/CH	CH/CH
Irradiated arrangements							
8	P_1	AR/AR	AR/AR	37	P_1	AR/AR	AR/AR
9	P_2	CH/CH	CH/CH	..			
10	F_1	CH/CH	AR/AR	48	B_{F1P2}	AR/CH	CH/CH
11	F_1	AR/AR	CH/CH				
12	F_2	AR/CH	AR/CH	49	P_1	AR/AR	AR/AR
13	F_2	AR/CH	AR/CH	..			
14	B_{F1P1}	AR/CH	AR/AR	55	B_{F1P2}	AR/CH	CH/CH

paper TANTAWY (1961) should be consulted. The various females obtained in the present experiment were mated with the same number of males of an appropriate genotype for the other parts of the experiments.

In the egg production experiment sixty virgin females were used in each of the irradiated groups for each dosage. During the collection of eggs, eggs were counted, collected and cultured for five successive days from the crosses of Table 1 for each radiation dosage as well as from controls in ordinary food bottles (not more than 150 eggs in each). After hatching the adults were counted and classified as to sex. For the study of body size, five females and five males from each bottle were measured on each of five days, giving a total of 175 pairs for controls and 1200 pairs for each of the irradiated dosages. Another five pairs on each day from each bottle were used for measuring body weight; the total number of flies was exactly the same as used for body size. In the longevity experiment 500 females from each of the

genotypes used in the egg production experiment were maintained for the estimation of survival and death rates.

The technical procedure followed in the present experiments were exactly the same as those reported by TANTAWY (1961). For more details concerning methods for egg collection, percentage of emergence, estimate of longevity, measurements of body size, body weight and the control of environmental variations also see TANTAWY (1961). In order to assure similar environmental conditions during the present work, great care was taken to ensure that all crosses were subjected to the same treatments. All the experimental work was carried out in incubators at 25 $\pm$ 0.5°C.

It is worthwhile to note that in the statistical analyses for percentage of emergence, body size and weight for the offspring resulting from crosses of Table 1 no significant differences were observed between the individuals of the same generation within dosage of radiation

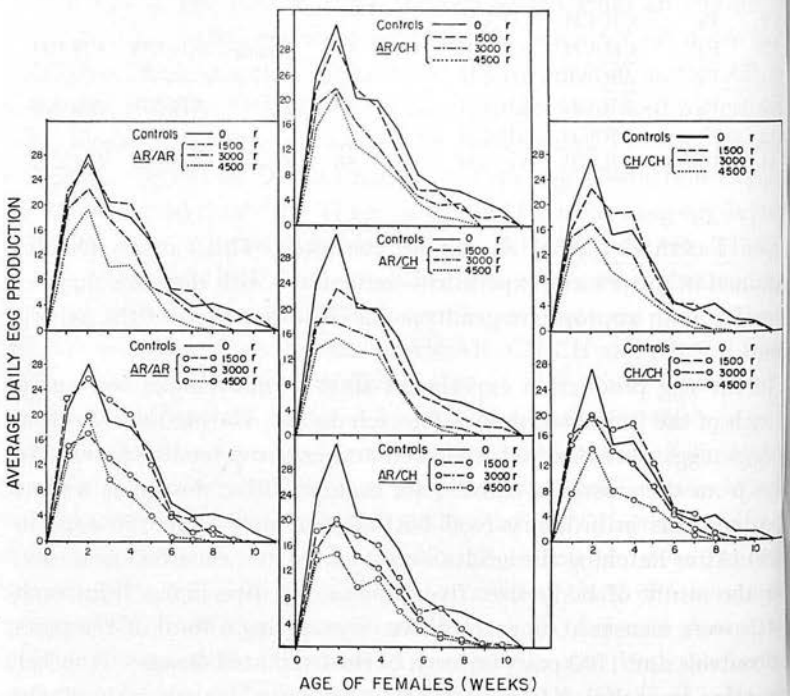

Fig. 1. Daily average lifetime egg production for control females and irradiated females of different gene arrangements. Each point represents the daily average in a given week.

whether they possessed 25%, 50% or more irradiated third chromosomes. Therefore for the sake of simplicity in the representation of the results, all data secured from the same generation with the same dosage were combined.

Results

Lifetime egg production

The relationship between egg production and genotype at various doses of X-irradiation is presented in Figure 1, as daily average per female in a given week. It can be seen that the highest peak for egg production in all the lines (with significant differences between them) occurred at the end of the second week of age, following which females showed a decline. Females from the control stock, as well as those carrying a third chromosome irradiated with 1500 r, laid eggs to the end of the eleventh week of age, while most of the other females laid eggs to the end of the eighth or ninth week of age.

Comparing the effects of different doses of radiation on egg laying capacity one notices that females carrying third chromosomes irradiated with 1500 r fluctuated around the control line while those

TABLE 2

AVERAGE DAILY LIFETIME EGG PRODUCTION PER FEMALE, WITH THEIR RESPECTIVE STANDARD ERRORS (± S.E.) AND COEFFICIENTS OF VARIATION (C.V.%)

Genotype	1500 r		3000 r		4500 r	
	Average	C.V.	Average	C.V.	Average	C.V.
AR/AR	12.40 ± 1.31	88.77	9.93 ± 1.31	104.15	7.15 ± 1.11 [3]	122.24
AR/CH	12.01 ± 1.39	97.34	9.96 ± 1.24	97.99	8.04 ± 1.17 [3]	115.05
AR/CH	11.05 ± 1.16	88.42	9.95 ± 1.17	93.14	7.54 ± 1.02 [2]	106.50
CH/CH	10.03 ± 1.10	92.32	7.57 ± 1.13 [1]	110.30	5.55 ± 0.89 [4]	118.38
AR/AR	11.26 ± 1.33	99.47	7.96 ± 0.94 [2]	94.47	6.26 ± 1.09 [4]	129.23
AR/CH	10.12 ± 1.10	91.40	9.33 ± 1.16	98.39	6.66 ± 0.97 [4]	114.71
CH/CH	9.71 ± 1.06	91.66	7.53 ± 1.08 [1]	112.88	5.16 ± 0.97 [4]	117.05
Controls: AR/AR	11.76 ± 1.30	(C.V. 91.50)				
AR/CH	11.98 ± 1.26	(C.V. 87.84)				
CH/CH	10.39 ± 1.48	(C.V. 100.58)				

Probabilities from controls:
[1] $< 0.1 > 0.05$ [2] $< 0.05 > 0.02$ [3] $< 0.02 > 0.01$ [4] $< 0.01 > 0.001$.

carrying chromosomes irradiated with 3000r or 4500r laid fewer eggs than did the controls; the poorest females in this respect were those carrying chromosomes irradiated with 4500r. In all groups (except the 1500r) heterozygous females laid more eggs than homozygous females of either AR/AR or CH/CH, with the latter being inferior to the former. The situation is different in females with the chromosomes irradiated with 4500r. The AR/AR and AR/AR females were superior, but not significantly so (see Table 2).

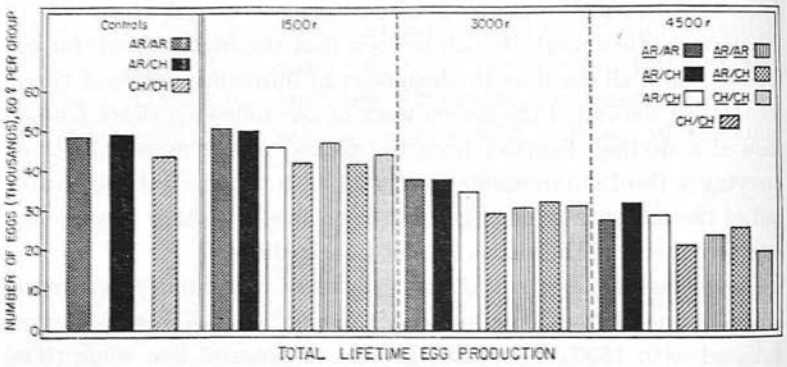

Fig. 2. Total lifetime egg production for control females and irradiated different gene arrangements (60 females in each group). P-values, based on the average production per female, between controls and irradiated ones, were not significant at 1500r. At 3000r, AR/AR, AR/AR, AR/CH, AR/CH, and AR/CH had a $P < 0.3 > 0.2$, CH/CH and CH/CH $< 0.2 > 0.1$; at 4500r, AR/CH and AR/CH $< 0.1 > 0.05$, AR/AR $< 0.02 > 0.01$, CH/CH, AR/AR, AR/CH and CH/CH $< 0.01 > 0.001$.

Figure 2 reports the total lifetime egg production. The results demonstrate that radiation with 1500r had no significant effect on egg laying capacity, while higher doses of radiation caused a significant decline in this character. The results also show significant differences among various genotypes at the same dose level, (test of significance from controls is shown in the caption of Figure 2). The egg production of heterozygous females, i.e. AR/CH, AR/CH and AR/CH with chromosomes irradiated with 1500r and 3000r were intermediate between the parental level, while the females with 4500r were higher than either parent. The superiority of the heterozygous over homozygous females will be discussed later.

The reduction in egg production at the higher doses of rediation is in agreement with the work reported by HERSKOWITZ & ABRAHAMSON (1956) and ABRAHAMSON & HERSKOWITZ (1957) who found a significant decrease in the fecundity of irradiated females of *D. melanogaster*, particularly at the higher doses of X-rays. GOWEN & STADLER (1952) demonstrated that the number of eggs laid by *D. melanogaster* irradiated with 2500r was not seriously altered. Above 2500r, however, there was a linear decline in egg production with increasing dose. The same linear relationship has been demonstrated by ANNAN (1955) in *D. robusta*.

Table 2 reports the daily average of egg production per female for her lifetime with respective standard errors and coefficients of variation. It can be seen that higher doses of radiation caused a significantly greater decline in egg production than did the lower doses. The percentage decline from the controls will be shown later. The results shown in Table 2 indicate clearly that the CH/CH and CH/CH females laid the fewest eggs, the differences between these two groups being significant. The AR/AR and AR/AR irradiated gene arrangements were superior, though not significantly so, to the heterozygous females at 1500r, but at higher doses the latter were superior to all other females.

The coefficients of variation shown in Table 2 indicate that most of the females with 1500r irradiated chromosomes showed a slight though insignificant increase in phenotypic variation as compared with the controls. All females carrying irradiated third chromosome at the higher doses of radiation showed greater variation in egg laying capacity than did the controls. It is interesting to note that heterozygous females with irradiated chromosomes showed variations intermediate between the parental groups, apart from AR/CH which with 1500r were more variable. Another point of interest is that the AR/AR females at 1500r and 3000r showed less variation for egg production than did CH/CH females, apart from CH/CH at 1500r, while at 4500r the situation was reversed.

Such results indicate clearly that irradiation of the third chromosome with higher doses increased significantly the phenotypic variation in egg production and that this result is a function of the different inversions on the third chromosome.

Percentage of emergence and sex-ratio

Viability was measured as percentage of emergence of adults from a given number of eggs cultured in an ordinary food bottle. The different crosses of Table 1 were used for culturing eggs. Table 3 reports the total number of eggs cultured for each cross and the percentage of emergence. Sex-ratio is also presented.

The results indicate significant effects of X-irradiation on the percentage of emergence. Test of significance indicates that all crosses with different doses showed significant differences at the level of 0.01. The results also demonstrate that there was a linear decline in this trait with increasing dosages of radiation. In all groups the F_1 generation showed a higher percentage of emergence than did the parental generation, while the F_2 showed a non significant decline from either P_1 or P_2. The superiority of the heterozygous individuals over homozygous ones will be discussed later.

In comparing the heterozygous groups in the control populations, it can be seen that crosses within the AR/AR gene arrangement showed a higher percentage of emergence, though not significantly so, than those within the CH/CH genotype. The situation is similar

TABLE 3

NUMBER OF EGGS CULTURED (A), PERCENTAGE OF EMERGENCE (B) AND SEX-RATIO (C). FOR TEST OF SIGNIFICANCE SEE TEXT.

Cross	A	B	C	Cross	A	B	C
a: Controls				*c: 3000 r*			
P_1	1167	65.30 ± 0.95	49.9	P_1	2611	39.60 ± 2.95	52.5
P_2	1620	63.71 ± 1.03	49.4	P_2	2595	38.52 ± 3.30	50.6
F_1	1144	75.34 ± 0.93	50.5	F_1	4790	46.36 ± 3.00	50.4
F_2	1517	62.79 ± 1.02	51.6	F_2	4377	40.18 ± 3.04	49.1
B_{F1P1}	2090	76.54 ± 0.99	50.6	B_{F1P1}	3321	40.49 ± 2.99	50.3
B_{F1P2}	1542	71.69 ± 1.02	49.5	B_{F1P2}	3214	36.88 ± 3.04	51.4
b: 1500 r				*d: 4500 r*			
P_1	3007	53.93 ± 2.00	50.1	P_1	2156	20.33 ± 3.51	48.3
P_2	2724	50.06 ± 2.13	51.3	P_2	1734	22.65 ± 3.40	47.4
F_1	5385	59.82 ± 2.01	52.0	F_1	3894	29.76 ± 3.41	48.0
F_2	4181	52.70 ± 2.11	50.9	F_2	3790	26.99 ± 3 50	47.4
B_{F1P1}	4126	58.01 ± 2.09	51.7	B_{F1P1}	3252	20.19 ± 3.49	46.3
B_{F1P2}	3730	54.01 ± 2.12	52.0	B_{F1P2}	2719	25.02 ± 3.33	47.5

for crosses given 1500r and 3000r, while with those given 4500r the situation was reversed. The F_1 females backcrossed to AR/AR males showed higher viability in the a, b, and c groups of Table 2 while in group d viability was higher in the backcross to CH/CH males. The percentage decline from the controls will be shown later.

The deleterious effects of X-irradiation on percentage of emergence could be attributed to higher egg mortality (HERSKOWITZ, 1957). The results obtained agree with the data reported by WALLACE (1951), KING (1952), CATCHESIDE & LEA (1945), YANDERS (1954) and PARKER (1959) who showed a negative correlation between direct X-ray dosage and viability in *Drosophila*.

Estimation of sex-ratio indicates that, in control populations as well as those carrying third chromosome irradiated with 1500r and 3000r, no significant differences occurred between sexes although females were in excess. However, with 4500r, males predominate

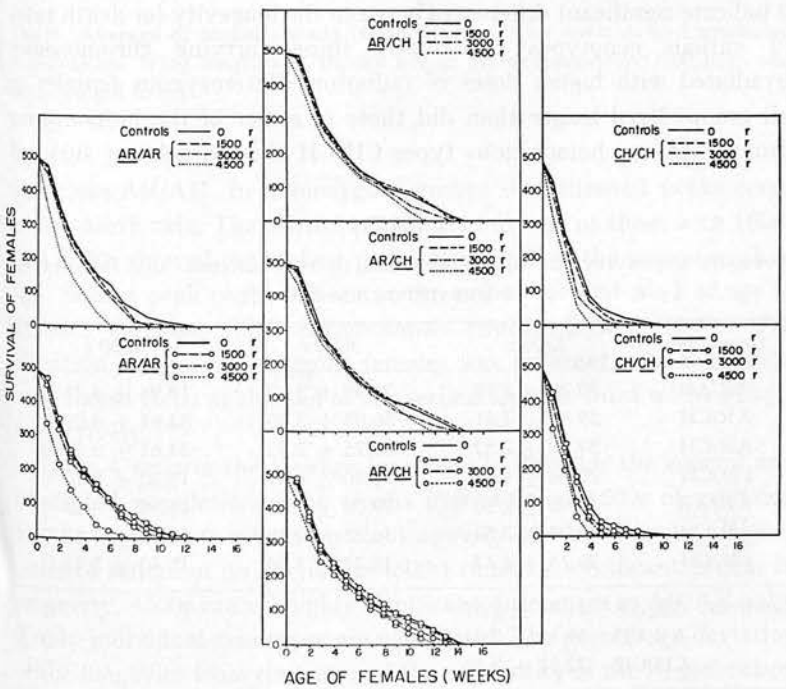

Fig. 3. Survival of females in the control populations and in the irradiated populations.

significantly ($P < 0.05$). The increase of males over females with higher doses of radiation agrees with the results of DEMEREC & FANO (1944) and CATCHESIDE & LEA (1945) who reported a significant shift in the male direction due to radiation.

Longevity

The existence of lethal effects of radiation is well known. In an experiment with direct gamma radiation on flour beetle, CORK (1957) showed that radiation, particularly at higher doses, could cause 100% lethality within twenty days. GOWEN & STADLER (1952) and BAXTER & TUTTLE (1957) found in *D. melanogaster*, that lifespan shortening was proportional to direct doses of X-rays.

The longevity of the adult females carrying the irradiated third chromosome is shown in Figure 3 as number of surviving females. Females used in this experiment are similar in their genotypes to those used in the egg production experiment. The results as shown in Figure 3 indicate significant differences between the longevity (or death rate) of various genotypes particularly those carrying chromosomes irradiated with higher doses of radiation. Heterozygous females in all groups lived longer than did those of either of the homozygous groups. Among homozygous types CH/CH showed a lower survival

TABLE 4

AVERAGE LONGEVITY (DAYS) FOR FEMALES IN THE CONTROL AND IRRADIATED POPULATIONS. N = 500

Genotypes	1500 r	3000 r	4500 r
AR/AR	30.28 ± 2.78	28.99 ± 3.12	18.96 ± 4.11 [3]
AR/CH	39.40 ± 2.41	36.95 ± 3.00	32.61 ± 4.00 [2]
AR/CH	39.80 ± 2.52	36.75 ± 2.92	34.61 ± 3.99 [1]
CH/CH	20.58 ± 4.01	18.90 ± 4.51	15.23 ± 5.12 [1]
AR/AR	31.65 ± 2.88	29.08 ± 3.21	18.98 ± 4.22 [1]
AR/CH	39.02 ± 2.54	36.13 ± 2.45	32.55 ± 3.49 [1]
CH/CH	20.73 ± 4.12	18.77 ± 3.98	15.43 ± 5.43 [1]
Controls: AR/AR	31.44 ± 2.57		
AR/CH	39.13 ± 2.21		
CH/CH	22.81 ± 3.78		

Probabilities from controls:
[1] $< 0.1 > 0.05$ [2] $< 0.05 > 0.02$ [3] $< 0.02 > 0.01$.

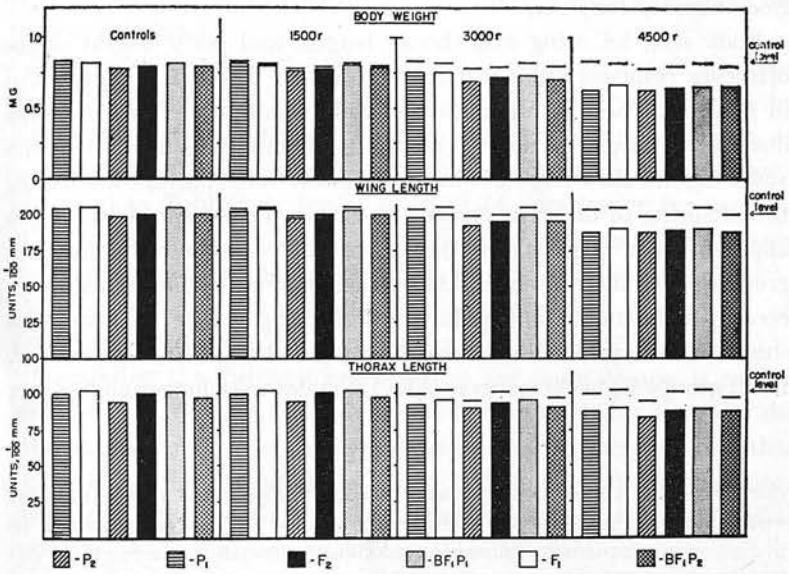

Fig. 4. Average of measurements (sexes averaged) for controls and irradiated populations. Wing length and thorax length are expressed in 1/100 m.m and body weight in mg.

rate than AR/AR. In homozygous groups two different peaks occur in the death rate. The control populations as well as those with 1500r and 3000r showed the highest peaks at the end of the second week of age. Such a peak could be seen at the end of the first week of age in females carrying third chromosomes irradiated with 4500r. The situation in the heterozygous females was different; the two peaks were found to be at the end of the second and the third weeks of age, respectively.

Table 4 reports the average longevity in days for the control and irradiated populations. The results indicate that 1500r of radiation had no significant effects on the longevity of adult females. Higher doses of radiation (in particular 4500r) caused a significant decline in longevity, 4500r caused highly significant differences in AR/AR only, if only individual genotypes are considered. The percentage deviation of the longevity from controls and the superiority of the F_1 generation over parental ones will be discussed later.

Body size and body weight

Body size, i.e. wing and thorax length, and body weight of the offspring resulting from different crosses of Table 1 are presented in Figure 4. These results indicate highly significant effects of higher doses of radiation on metric characters. Populations irradiated with 1500r did not show any significant deviation from controls. Comparing the offspring of different crosses at various doses of radiation, it is apparent that offspring of the crosses between both homozygous groups gave values intermediate between parental generations for the control and irradiated populations. Offspring in the F_2 generation showed a decrease in size and weight compared with the F_1 generation. In all groups F_1 backcrosses to AR/AR males were longer and heavier

TABLE 5

VARIANCE ($\sigma^2 \times 10^6$) OF LOGARITHMS OF MEASUREMENTS (SEXES AVERAGED) FOR WING LENGTH, THORAX LENGTH AND BODY WEIGHT IN THE CONTROL AND IRRADIATED POPULATIONS. FOR TEST OF SIGNIFICANCE SEE TEXT

Crosses	Controls	1500 r	3000 r	4500 r
Wing length:				
P_1	133	149	192	676
P_2	152	164	246	627
F_1	133	148	173	474
F_2	148	176	345	662
B_{F1P1}	115	143	176	429
B_{F1P2}	121	149	254	589
Thorax length:				
P_1	383	385	661	1711
P_2	483	509	1316	2649
F_1	353	361	449	736
F_2	532	535	684	1374
B_{F1P1}	402	419	498	1720
B_{F1P2}	441	522	971	1713
Body weight:				
P_1	2006	2139	2929	4268
P_2	2369	2655	3270	3869
F_1	1574	1606	2553	2876
F_2	1841	1937	2726	3900
B_{F1P1}	983	1189	1628	3312
B_{F1P2}	1527	1569	2289	2789

than those backcrossed to CH/CH males. The percentage decline from controls and the increase of the F_1 over the parental generation will be discussed later.

The variance (σ^2) of the logarithms of measurements are given in Table 5. Variance of logarithms have been used, as reported by TANTAWY (1961), to cancel out the effects of mean body size on variance as these are often positively correlated. The variance as presented in Table 5 indicates (by test of significance for equality of variance) that with 1500r no significant differences exist between the controls and irradiated populations. Radiation with 3000r and 4500r, caused a highly significant increase in the variance of all groups for all characters (P values for 3000r and 4500r < 0.001).

Comparing the different genotypes at the same dosage, it can be seen that the F_1 generation showed a lower variability than did the other crosses, while the F_2 generation showed an increase over that of the F_1. In all groups AR/AR populations showed less variation, apart from wing length and body weight at 4500r, than the CH/CH populations. F_1 females backcrossed to AR/AR males showed in general less variation in all characters than those backcrossed to CH/CH males. There are, however, some exceptions where the former backcross showed less variation as for example, in thorax length and body weight in populations treated with 4500r.

Discussion and conclusions

The experiments performed provide information on the effects of different dosages of X-irradiation, on components of fitness as well as on some metric characters. Third chromosomes irradiated with 1500r showed significant effects only on percentage of emergence, while with 3000r and 4500r there were highly significant effects on all traits studied. In the following discussion three main topics of the effects of X-rays irradiation will be considered: percentage deviation from controls, heterosis and adaptive fitness.

Percentage deviation from controls

It has been shown by many investigators that lower doses of X-irradiation do not affect significantly the character or characters under consideration. For instance, ABRAHAMSON & HERSKOWITZ

(1957) found in *D. melanogaster* that dosages lower than 2500r did not influence appreciably the number of eggs laid, while higher doses resulted in a considerable decrease.

Results obtained from the present study are presented in Tables 6 and 7 as percentage deviations from controls for egg production, longevity, percentage of emergence, body size and body weight. The results thus presented indicate clearly that lower doses of radiation have no stistically significant effects on any of the characters studied except the percentage of emergence which is significantly decreased. It would seem of some interest to state that the deviations of females carrying irradiated chromosomes from controls are nearly all in the minus direction. In fact whilst no individual deviation is statistically significant 30 of the 34 comparisons show a deviation in the minus direction and the probability that this is a chance effect, is very low indeed. Thus it is not safe to say that 1500r has no effect on the characters studied. This decrease in percentage of emergence with lower doses of radiation could be explained on the basis that irradiation

TABLE 6

PERCENTAGE DEVIATIONS ± S.E. FROM CONTROLS FOR EGG PRODUCTION (BASED ON DAILY AVERAGES) AND LONGEVITY, FOR THE IRRADIATED POPULATIONS. THIRD CHROMOSOMES OF IRRADIATED ANCESTRY ARE UNDERLINED

Genotype	1500 r	3000 r	4500 r
Egg production:			
AR/AR	+ 5.44 ± 2.41	− 15.56 ± 3.18	− 39.20 ± 4.12
AR/CH	− 0.25 ± 2.11	− 16.86 ± 3.01	− 32.89 ± 4.81
AR/CH	− 7.76 ± 3.94	− 16.94 ± 3.51	− 37.06 ± 4.95
CH/CH	− 3.46 ± 3.09	− 27.14 ± 4.51	− 46.58 ± 5.14
AR/AR	− 4.25 ± 3.41	− 32.31 ± 4.11	− 46.77 ± 5.67
AR/CH	− 15.53 ± 4.90	− 22.12 ± 3.89	− 50.34 ± 5.82
CH/CH	− 6.54 ± 4.81	− 27.53 ± 4.32	− 44.41 ± 6.31
Longevity:			
AR/AR	− 3.69 ± 1.21	− 7.79 ± 1.53	− 39.69 ± 2.84
AR/CH	+ 0.69 ± 1.41	− 5.57 ± 2.31	− 16.66 ± 3.21
AR/CH	+ 1.71 ± 1.22	− 6.08 ± 2.05	− 11.55 ± 2.95
CH/CH	− 9.78 ± 3.12	− 17.14 ± 3.21	− 33.23 ± 3.99
AR/AR	+ 0.67 ± 1.45	− 5.93 ± 2.11	− 39.63 ± 3.02
AR/CH	− 0.28 ± 1.04	− 7.67 ± 2.01	− 17.33 ± 3.10
CH/CH	− 9.12 ± 3.44	− 17.71 ± 3.95	− 32.35 ± 4.11

increased the egg mortality (HERSKOWITZ, 1957), due to an increase in dominant lethal mutations (CATCHESIDE & LEA, 1945). The results also indicate (Table 6) that in *D. pseudoobscura* dosages lower than 1500r should have insignificant effects on production rate as measured by egg laying capacity. Dosages as high as 3000r or more have significant effects on oviposition. These results agree fairly well with those reported by GOWEN & STADLER (1952), ABRAHAMSON & HERSKOWITZ (1957) and others who found no effects on oviposition rate in *D. melanogaster* females given lower doses. On the other hand, ANNAN (1955) reported that in *D. robusta* dosages as low as 2500r cause a decline in egg production. The results of Table 6 illustrate that, in the heterozygous individuals irradiation of the CH gene arrangement with 1500r or 3000r show more reduction (though insignificant) than

TABLE 7

PERCENTAGE DEVIATIONS ± S.E. FROM CONTROLS FOR PERCENTAGE OF EMERGENCE, BODY SIZE AND BODY WEIGHT FOR THE PROGENY OF THE IRRADIATED CROSSES

Cross	Percentage of emergence	Body size		
		Wing length	Thorax length	Body weight
1500 r				
P_1	− 17.41±1.05	− 0.56±0.03	− 0.90±0.05	− 0.48±0.03
P_2	− 21.43±1.13	− 0.26±0.04	− 0.54±0.06	− 0.65±0.04
F_1	− 20.60±1.09	− 0.88±0.03	− 2.60±0.03	− 0.87±0.05
F_2	− 16.07±1.12	− 0.29±0.04	− 1.11±0.07	− 0.64±0.03
B_{F1P1}	− 24.21±1.20	− 1.05±0.09	− 1.35±0.08	− 1.72±0.04
B_{F1P2}	− 24.66±1.25	− 0.12±0.09	− 0.42±0.10	− 0.38±0.04
3000 r				
P_1	− 39.36±2.00	−2.92±0.05	− 6.57±0.11	− 9.03±0.05
P_2	− 39.54±3.14	− 2.99±0.07	− 4.71±0.12	− 11.50±0.06
F_1	− 38.47±2.90	− 2.90±0.05	− 7.84±0.10	− 6.20±0.05
F_2	− 36.01±3.02	− 2.94±0.07	− 6.78±0.12	− 7.18±0.06
B_{F1P1}	− 47.10±3.11	− 3.31±0.09	− 7.12±0.13	− 9.45±0,08
B_{F1P2}	− 48.56±3.14	− 3.20±0.11	− 6.33±0.14	− 9.82±0.09
4500 r				
P_1	− 68.87±3.09	− 7.95±0.12	− 12.61±0.15	− 24.07±0.17
P_2	− 64.45±3.09	− 5.83±0.14	− 11.31±0.15	− 18.35±0.16
F_1	− 60.50±3.00	− 6.93±0.14	− 14.09±0.13	− 18.61±0.17
F_2	− 57.02±3.15	− 6.38±0.17	− 13.62±0.14	− 18.33±0.19
B_{F1P1}	− 73.62±3.15	− 7.67±0.19	− 14.92±0.92	− 20.66±0.21
B_{F1P2}	− 65.10±3.17	− 6.98±0.18	− 11.05±0.17	− 17.86±0.20

if AR is irradiated, while with 4500r for longevity the situation is reversed.

Comparing the two homozygous groups (Table 7) we see that the CH/CH populations irradiated with 1500r and 3000r showed a greater (though not significantly) reduction in most of the crosses compared with AR/AR, while with 4500r the situation is often reversed in favour of CH/CH. The F_2 generation showed an unexpectedly smaller reduction than the F_1 in all the characters studied except wing length and body weight with 3000r. Comparing the backcrosses one can see that with 1500r and 3000r neither group tends to be lower than the other, but with 4500r, F_1 females backcrossed to CH/CH males show less reduction than those backcrossed with AR/AR males. These results are interesting since TANTAWY (1961) used the same populations and the same crosses maintained at various temperatures and reported that the CH/CH gene arrangement is superior to the AR/AR one at higher temperatures, while the latter is superior at lower ones. From the results of the present experiments and those reported previously by the author one can conclude that the gene arrangement which is superior at higher temperatures may be less affected by higher dosages of irradiation than gene arrangements favoured by lower temperatures. Such a point needs more experimental work to be clarified and should be investigated on natural populations of *Drosophila* captured from different geographical regions.

Heterosis

Heterosis is measured as percentage deviations of F_1 or F_2 from parental average (TANTAWY, 1957) of the same irradiated gene arrangements. The results are listed in Table 8. It seems likely that irradiation of the third chromosome in *D. pseudoobscura* populations, caused greater heterosis in populations given 4500r than in those given lower doses. No significant difference were found between the control populations and those irradiated with 1500r. With 3000r and 4500r the percentage of heterosis increased in all characters with significant differences at 4500r, except for body size in which heterosis is less than that found in the control populations. At all dosages the F_2 generation shows a breakdown in heterosis.

TABLE 8

PERCENTAGE HETEROSIS IN F_1 AND F_2 GENERATIONS, IN THE CONTROL AND IRRADIATED POPULATIONS

Character		Controls	1500 r	3000 r	4500 r
Egg prod.	F_1	8.12±5.17	1.93±6.71	18.18± 7.52	22.89± 8.91
	F_2	—	—	—	—
% Emerg.	F_1	16.79±3.51	15.06±4.33	18.69± 4.81	38.48± 5.44
	F_2	− 2.65±3.90	1.37±4.90	2.87± 4.91	25.59± 5.90
Longevity	F_1	44.23±5.53	52.69±8.92	52.16±10.11	93.53±15.14
	F_2	—	—	—	—
Wing l.	F_1	1.83±0.32	1.35±0.52	1.89± 0.74	1.80± 1.11
	F_2	− 0.33±0.41	− 0.20±0.79	− 0.31± 0.92	0.24± 1.41
Thorax l.	F_1	7.59±1.91	5.01±2.14	5.11± 2.24	5.01± 0.54
	F_2	3.80±2.11	2.86±2.41	2.57± 2.54	1.87± 2.53
Weight	F_1	0.37±0.53	0.13±0.66	4.85± 0.95	3.96± 1.05
	F_2	− 2.86±0.95	− 2.88±1.42	0.41± 1.13	0.95± 1.27

The results as reported in Table 8 indicate that in the F_1 hybrid, heterosis is not found to the same degree in all characters studied; obvious fitness components display the highest percentage of heterosis. The highest heterosis is most obvious in the most unfavourable conditions, i.e. in the irradiated populations with 4500r. It is interesting to note that the effects of high dosages of radiation showed a pattern comparable to that of higher temperatures as shown by WALLACE (1948) and TANTAWY (1961) in *Drosophila* populations.

Adaptive values

The relative fitness of P_1, P_2 and F_1 of the controls and irradiated third chromosome populations are presented in Table 9. The unirradiated heterozygous genotypes were arbitrarily given the fitness 1.00. No differences in the adaptive values were found between the controls and 1500r irradiated populations. For controls the order of the adaptive values was AR/CH > AR/AR > CH/CH in all the fitness traits. With higher dosages of radiation, adaptive values declined. With 4500r the order was $\underline{AR}$/CH > AR/$\underline{CH}$ > $\underline{AR}$/AR > $\underline{CH}$/CH for all characters except for longevity where AR/$\underline{CH}$ > $\underline{AR}$/CH. With both gene arrangements irradiated, the order of the adaptive

TABLE 9

THE RELATIVE FITNESS FOR CONTROL AND IRRADIATED POPULATIONS WITH DIFFERENT GENE ARRANGEMENTS

Character	AR/AR	AR/CH	AR/CH	CH/CH	AR/AR	AR/CH	CH/CH
1500 r							
Egg prod.	1.03	1.00	0.92	0.84	0.94	0.85	0.81
% Emerg.	0.65	0.99	0.94	0.54	0.69	0.92	0.60
Longevity	0.77	1.01	1.02	0.53	0.81	0.10	0.53
3000 r							
Egg prod.	0.83	0.83	0.83	0.63	0.66	0.78	0.63
% Emerg.	0.52	0.73	0.71	0.39	0.53	0.69	0.39
Longevity	0.74	0.94	0.94	0.48	0.76	0.92	0.48
4500 r							
Egg prod.	0.60	0.67	0.63	0.46	0.52	0.56	0.43
% Emerg.	0.39	0.44	0.40	0.28	0.26	0.46	0.43
Longevity	0.48	0.83	0.88	0.39	0.48	0.83	0.39

Controls:	AR/AR	AR/CH	CH/CH
Egg production	0.98	1.00	0.87
% Emergence	0.87	1.00	0.85
Longevity	0.80	1.00	0.58

values was, for 4500r, AR/CH > AR/AR > CH/CH, except the percentage of emergence where CH/CH > AR/AR. It would be interesting to run population cages with different irradiated gene arrangements with various doses to see whether equilibrium frequency of the inversion would correspond to the fitness components as they do with 4500r, where CH/CH is often superior to AR/AR. The decline in the adaptive values particularly with higher doses may be due to new gene combinations arising by radiation as radiation may affect the rate of crossing-over as well as the kind of genetic units present. Such results are in agreement with those reported by WALLACE & KING (1951) who found that irradiation of the second chromosome in *D. melanogaster* caused a decrease in adaptive value.

Comparing the results of the present study with those reported by TANTAWY (1961), one may conclude that some relationship exists between adaptation to higher temperature and the depression effects of higher doses of radiation. Further detailed investigations are needed and the use of populations from Lebanon and Uganda which

showed different adaptation to various temperatures (TANTAWY & MALLAH, 1961) would be of value.

The second point of interest that can be derived from the present studies is the relationship between variability and fitness. It is generally clear that greater fitness is associated with lower variability (Tables 2, 3 and 4). The superior gene-arrangement within each dosage of radiation produces less phenotypic variability both for fitness and metric characters, although the differences are not significant. The picture is, however, the same when variability within dosages, averaged for the three dosages, is considered. For average daily egg production (Table 2) the coefficients of variation of the genotypes AR/AR, AR/CH, AR/CH, CH/CH, AR/AR, AR/CH and CH/CH are: 105.05, 103.46, 96.02, 107.00, 107.72, 101.50 and 107.20, respectively. The corresponding values between dosages for the controls are: 87.84, 91.50 and 100.58 for the genotypes AR/CH, AR/AR and CH/CH, respectively. It is also of interest to note that irradiation of both gene-arrangements resulted in more phenotypic variation in such a character than if only one gene-arrangement was irradiated.

The increase in the phenotypic variation by irradiation may indicate that higher doses of X-rays increase the response to artificial selection for a given quantitative character. Such an increase in the response could be due to increase of the genetic variability by increasing mutation rate (IVES, 1959). Response to selection in irradiated populations of *D. melanogaster* has been investigated by SCOSSIROLI (1954). He concluded that X-ray treatment was effective in producing new variability in the polygenic system related to the selected trait, and that artificial selection was able to utilize such an increase. The relation of such an induced variability, the nature of which is still obscure, to dosage should be investigated.

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EFFECTS OF TEMPERATURE AND X-RAY IRRADIATION ON INTRINSIC GROWTH RATE IN POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*

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An experiment was designed using populations of *Drosophila pseudoobscura* with different gene arrangements on the third chromosome, to study the effects of various temperatures and different dosages of radiation on the innate capacity for increase.

The innate capacity for increase was found to increase with temperature and decrease with higher in radiation dosages. The mean generation length showed a decline with both treatments with a greater decrease in the former treatments.

Net reproductive rate showed a decrease in both cases while the finite rate of increase (λ) showed an increase in the temperature experiment and a decrease in the radiation experiment.

Percentage contribution of each age group to the rate of muliplication per generation depends on temperature and dosages of radiation as well as the genetic background of the population.

Introduction

The capacity of a given population to grow in size is mainly determined by its innate capacity for increase and by environmental conditions. Therefore, the innate capacity for increase fluctuates widely according to fluctuations in environmental conditions. Each animal raised in a given environment grows and produces offspring for a certain time, after which it ceases to produce, either because of infertility or death.

In the determination of the innate capacity of increase of a given population, i.e. the rate of multiplication, it is essential to know the survival rate or death rate and the age schedule of fecundity (BIRCH 1948). The first complete life-tables for *Drosophila melanogaster* were those published by PEARL & PARKER (1921) for normal wild type and the mutant *vestigial*. In subsequent papers (1922; 1924) they dealt with the effects of different environmental factors on

e-tables. Other early publications, e.g. those of GONZALEZ (1923) d ALPATOV & PEARL (1929) working on *Drosophila melanogaster* ould be consulted.

LOTKA (1925) was the first to attempt the calculation of the rate increase in human populations and arrived at a function which called "the intrinsic rate of natural increase or r_m "to take into nsideration the change in birth and death rates with advance age. The function r_m was used by LESLIE & RANSON (1940) in imal ecology, BIRCH (1948; 1953 a, b), LESLIE & PARK (1949), VANS & SMITH (1952) and HOWE (1953 a, b) in insect populations. The present communication is concerned with the effects of differt temperatures and various doses of X-rays on the intrinsic rate of crease of *Drosophila pseudoobscura* populations of different genetic ackgrounds.

Material and Methods

Two populations of *Drosophila pseudoobscura*, one homozygous or the Arrowhead (AR/AR) and the other for the Chiricahua (CH/CH) ene arrangements of the third chromosome, kept for almost two ears (temperature experiment) and for three years (radiation xperiment) in population cages, were used as material for the present udies. TANTAWY (1961) reported the origin, locality and crosses ade for the maintainance of these populations and methods for ntrol of environmental variations. Two different experiments ere performed:

Temperature experiment

Three different temperatures were used, viz., 15°C., 25°C., and 7°C. Crosses were made between and within various populations to btain virgin females of AR/AR, AR/CH and CH/CH karyotypes to e used in lifetime egg production and longevity experiments. For easuring the egg production, 90 females (18 replicates, with five males in each) of each genotype were used at each temperature. n the longevity experiment 500 females were used per genotype en replicates with 50 females in each, for each genotype at each mperature) and death rate and survival rate were calculated. ANTAWY (1961) reported fully the design of such an experiment

and the paper should be consulted for details concerning the stocks and crosses and for the estimation of lifetime egg production and longevity.

b. Radiation experiment

The populations used in the temperature experiment were used also for the radiation study. Three different doses of X-rays, 1500 r, 3000 r, and 4500 r were given to different batches of AR/AR and CH/CH males. An unirradiated populations of the genotypes AR/AR, AR/CH, and CH/CH were used as controls. Irradiated males of either AR/AR or CH/CH were crossed with virgin females of *Bl Sc/L* for two generations after which the desired females carrying one irradiated third chromosome were obtained. For more details of radiation methods and crosses, see TANTAWY (1962). Females used for lifetime egg production were: AR/AR, AR/CH and CH/CH karyotypes for controls, and AR/AR, AR/CH, AR/CH, CH/CH, AR/AR, AR/CH and CH/CH for experimental karyotypes, where underlining indicates chromosomes descended from irradiated stock. All experiments were done in incubators kept at 25 ± 0.5°C.

The total number of females used in the egg production experiment was 60 (12 replicates, five females in each vial) for each of the seven irradiated genotypes at each dosage of radiation and 500 (ten replicates with 50 females in each bottle) of each genotype were used at each radiation dosage level to measure the death rate or survival rate. The methods for collecting eggs and measuring longevity were essentially the same as those used in the temperature experiment (TANTAWY, 1961).

In the present work, the statistical analyses applied to the data are the same as those reported by BIRCH (1948) on the assumption that sexes are equally frequent. However, all the analyses of the data obtained from 27°C and with 4500 r were corrected for differences in sex-ratio since females were significantly in excess of males (TANTAWY, 1961; 1962).

Results

The data required for the calculation of the innate capacity for increase (r_m) in a population are:

The survival rate of females alive at age (x), designated as l_x. The oviposition rate of a female aged (x), designated as m_x. Therefore, the calculation of r_m should equal to:

$$r_m = \frac{\log_e R_0}{T}$$

here, R_0 = the net reproductive rate = $\Sigma l_x m_x$

and, T = generation length = $\frac{\Sigma x l_x m_x}{\Sigma l_x m_x}$.

Reference should be made to BIRCH (1948) who explained the mathematical analyses to approach this problem in a very clear and lucid manner.

Effects of temperature on multiplication per generation

The original data for survival and therefore longevity and egg production for a given week were reported by the author elsewhere (TANTAWY, 1961 and 1962 for the temperature and radiation experiments, respectively). The calculations of $l_x m_x$ as presented in the following tables can be worked out from the data as presented previously by the author.

Table 1 reports the net reproductive rate ($R_0 = \Sigma l_x m_x$) and percentage contribution for each age group maintained at 15°C, 25°C, and 27°C, while Table 2 shows the muliplication per generation. The results as shown in Table 1 indicate clearly that at 15°C the CH/CH karyotype contributes at the end of the first week of age, a higher percentage than all other groups; AR/AR contributes the least, while at 25°C the situation is reversed. At 27°C AR/CH shows the highest contribution and CH/CH the least. The percentage contribution for each age group is different at different temperatures, i.e. 90% or more of the contribution can be obtained after the fourth, second and first week of age for the gene arrangements kept at 15°C, 25°C and 27°C, respectively.

The net reproductive rate which is the rate of multiplication in the generation (LOTKA, 1925) is shown in Tables 1 and 2. The net reproductive rates for the genotypes AR/AR, AR/CH and CH/CH

TABLE 1

NET REPRODUCTIVE RATE ($R_0 = \Sigma l_x m_x$) AND PERCENTAGE CONTRIBUTION OF EACH AGE GROUP AT DIFFERENT TEMPERATURES FOR ADULT STAGE

Age in weeks (x)	AR/AR $l_x m_x$	AR/AR % Contribution	AR/CH $l_x m_x$	AR/CH % Contribution	CH/CH $l_x m_x$	CH/CH % Contribution
15°C						
1	6.85	48.97	5.08	41.23	2.66	54.02
2	9.23	26.83	8.48	34.18	2.87	26.73
3	9.47	12.12	8.44	15.59	2.62	10.97
4	7.61	9.72	6.40	5.53	2.91	5.47
Σ 5–15	28.20	2.36	16.21	3.47	5.38	2.81
Total	Σ 61.36 [3]	100.00	44.61 [2]	100.00	16.44 [1]	100.00
25°C						
1	14.58	94.43	11.88	80.41	18.57	86.43
2	9.37	4.37	10.28	16.82	5.17	12.56
3	4.57	1.14	7.04	2.68	1.86	0.96
4	2.57	0.05	4.70	0.04	0.44	0.05
Σ 5–10	2.49	0.01	3.73	0.05	0.19	0.00
Total	Σ 33.58	100.00	37.63	100.00	26.23	100.00
27°C						
1	3.32	95.56	5.90	97.28	5.88	92.57
2	0.97	4.43	0.87	2.71	2.33	7.33
3	0.02	0.01	0.10	0.01	0.15	0.10
Σ 4–5	0.00	0.00	0.00	0.00	0.00	0.00
Total	Σ 4.31 [3]	100.00	6.87 [3]	100.00	8.36 [3]	100.00

Test of significance for 15°C and 27°C as compared with optimal temperature:
[1] $P < 0.05$ [2] $P < 0.01$ [3] $P < 0.001$

are given by the Totals in table 1. These results indicate different multiplication rates between temperatures and between genotypes within the same temperature. Thus, the AR/AR gene arrangement shows the highest multiplication at 15°C and CH/CH the least; the situation at 27°C is reversed. At 25°C the heterozygous genotype shows the highest multiplication and CH/CH the least ($P < 0.05$). The comparisons between different gene arrangements for the R_0

n the basis of mean generation length are presented in Table 2 here the finite rate of increase or λ which equals antilog$_e$ r_m, is erived from the intrinsic rate of increase which indicates the muli- lication per female per week. The results show that λ is significantly

TABLE 2

ATE OF INCREASE IN DIFFERENT POPULATIONS AT VARIOUS TEMPERATURES

enotypes	Intrinsic rate of increase (r/day)	Mean generation length in weeks (T)	Net reproduction rate (R_0)	λ *) Antilog$_e$ r_m
5°C				
AR/AR	0.844	4.88	61.36	2.32
AR/CH	0.759	5.01	44.61	2.14
CH/CH	0.805	4.72	16.44	2.23
5°C				
AR/AR	1.634	2.15	33.58	5.10
AR/CH	1.463	2.48	37.63	4.31
CH/CH	1.552	2.09	26.23	4.71
7°C				
AR/AR	1.196	1.23	4.31	3.31
AR/CH	1.662	1.16	6.87	5.25
CH/CH	1.611	1.32	8.36	5.00

*) For test of significance see text

ower ($P < 0.001$) at a colder temperature and significantly higher $P < 0.01$) at warmer ones, as compared with that found at the ntermediate temperature, i.e. 25°C, thus indicating a positive orrelation between the values of λ and temperature. The calculations f λ indicate that at 15°C carriers of the AR/AR gene arrangement ncrease at a greater rate than carriers of the CH/CH one, while t 27°C the latter is the dominant one.

. Effects of radiation on multiplication per generation

Table 3 shows the net reproductive rate and percentage contri- ution of each age group for controls and different irradiated gene rrangements. The control populations show almost the same trend in

TABLE 3a

NET REPRODUCTIVE RATE ($R_0 = \Sigma\, l_x m_x$) AND PERCENTAGE CONTRIBUTION OF EACH AGE GROUP IN THE CONTROL POPULATIONS

Age in weeks (x)	AR/AR		AR/CH		CH/CH	
	$l_x m_x$	% Contrib.	$l_x m_x$	% Contrib.	$l_x m_x$	% Contrib.
1	9.89	77.79	11.71	76.44	7.93	79.37
2	9.97	19.34	12.65	20.57	7.55	18.19
3	4.99	2.39	5.81	2.40	2.74	1.88
4	3.52	0.41	4.80	0.50	1.45	0.43
Σ 5–10	3.35	0.06	6.17	0.09	0.96	0.13
Total	31.72	100.00	41.14	100.00	20.63	100.00

percentage contribution as those reported at 25°C in the previous experiment (Table 1). The net reproductive rate of females carrying third chromosomes irradiated with 1500 r are similar to those of the controls, while those with 3000 r and 4500 r have a significantly lower net reproductive rate (test of significance is at the end of Table 3b).

Comparing the different genotypes within dosage of radiation, there are no significant differences (by t-test) between controls for the contribution at the end of the first week of age. Percentage contribution with increasing age shows a decline compared with the control population; this is statistically insignificant with 1500 r, but with 3000 r and 4500 r all irradiated gene arrangements show a significant decline.

In all the four groups 90% or more of the contribution is attained at the end of the second week of age, thus agreeing with the results obtained at 25°C (Table 1). The net reproductive rate (Tables 3 and 4) in the controls AR/AR, AR/CH and CH/CH are: 31.72, 41.14 and 20.63, respectively. Populations given 1500 r show almost the same values and relative order of karyotypes as those found in the controls. Females given 3000 r and 4500 r show the same order but with lower reproductive rates as compared with the controls, particularly those given the higher dosages. It is worthwhile to note that irradiation of both gene arrangements produces lower reproductive rates than if one is irradiated. In heterozygous individuals irradiation

TABLE 3b

ET REPRODUCTIVE RATE $R_0 = \Sigma l_x m_x$ AND (BETWEEN BRACKETS) PERCENTAGE CONTRIBUTION OF EACH AGE GROUP IN THE IRRADIATED POPULATIONS

ge in veeks (x)	AR/AR	AR/CH	AR/CH	CH/CH	AR/AR	AR/CH	CH/CH
500 r							
1	10.20	10.60	8.29	7.53	10.67	8.82	7.17
	(75.34)	(74.46)	(70.34)	(81.36)	(75.71)	(70.86)	(72.75)
3	9.62	11.23	8.88	6.09	8.85	7.34	5.10
	(18.58)	(19.11)	(20.98)	(15.16)	(18.48)	(20.71)	(19.83)
3	5.22	6.22	5.75	3.20	5.46	4.85	2.91
	(4.58)	(4.81)	(6.13)	(2.83)	(4.42)	(5.99)	(5.40)
4	3.98	4.53	4.76	1.45	4.11	3.88	1.33
	(1.13)	(1.21)	(1.79)	(0.53)	(1.06)	(1.73)	(1.47)
Σ5–10	3.40	4.30	4.94	0.54	2.90	4.51	0.53
	(0.37)	(0.41)	(0.76)	(0.12)	(0.33)	(0.71)	(0.55)
Total (100.00)	32.42	36.88	32.62	18.81	31.99	29.40	17.04
000 r							
1	9.08	9.11	8.73	6.39	7.07	8.29	6.32
	(76.13)	(74.08)	(71.63)	(77.36)	(73.01)	(72.08)	(76.12)
2	7.53	8.40	6.79	4.31	5.43	6.49	4.69
	(18.22)	(19.20)	(20.94)	(17.33)	(20.10)	(18.87)	(18.22)
3	4.19	4.63	4.73	1.28	2.94	3.99	1.58
	(4.31)	(4.98)	(5.48)	(4.01)	(5.65)	(7.21)	(4.32)
4	2.44	2.97	3.55	0.60	1.88	2.66	0.74
	(1.02)	(1.29)	(1.44)	(0.92)	(0.58)	(1.35)	(1.02)
Σ5–10	1.61	3.13	2.27	0.18	1.92	2.06	0.20
	(0.32)	(0.45)	(0.51)	(0.27)	(0.66)	(0.49)	(0.32)
otal (100.00)	24.85 [1]	28.24 [1]	26.07 [2]	12.76 [1]	19.24 [2]	23.49 [2]	13.53 [1]
500 r							
1	5.05	6.60	6.31	4.01	4.28	5.82	2.51
	(72.80)	(71.84)	(68.87)	(72.32)	(60.86)	(70.97)	(65.01)
2	4.30	6.82	5.10	2.76	4.26	4.64	2.94
	(19.64)	(20.18)	(21.37)	(19.91)	(20.71)	(19.93)	(22.75)
3	1.51	3.14	3.45	0.55	1.56	2.30	0.48
	(5.46)	(5.72)	(6.70)	(5.59)	(5.99)	(6.25)	(7.96)
4	0.95	2.12	2.78	0.04	0.66	2.22	0.07
	(1.52)	(1.62)	(2.10)	(1.57)	(1.74)	(1.96)	(2.79)
5–6	0.33	2.09	2.40	0.03	0.20	1.76	0.07
	(0.58)	(0.64)	(0.96)	(0.61)	(0.70)	(0.89)	(1.49)
otal (00.00)	12.14 [2]	20.17 [3]	20.04 [3]	7.39 [3]	10.96 [3]	16.74 [3]	6.07 [3]

Test of significance from controls:
[1]) $P < 0.01$ [3]) $P < 0.01$ [3]) $P < 0.001$

of the CH gene arrangement produces a lower value than if the AR one is irradiated.

The calculations of λ (Table 4) indicate that there is a negative correlation between the values of λ and dosage of radiation. With higher dosages, the number of offspring per female per week declines, thus indicating that higher doses of radiation cause a decrease in the capacity of the population to increase in number. CH/CH populations show the greater decrease especially when both chromosomes are irradiated and the heterozygous genotypes are often superior to homozygotes.

c. Effects of temperature and irradiation on innate capacity for increase

Tables 2 and 4 report the intrinsic rate of increase (r_m), mean generation length (T), net reproductive rate (R_0), and λ for all karyotypes for females kept at various temperatures and females carrying third chromosomes irradiated with different dosages of radiation. The intrinsic rate of increase has been defined as the rate of increase per head under specified physical conditions and when the possible effects of increasing density do not need to be considered (BIRCH, 1948). Such a measurement for a given population maintained at different environmental conditions should provide measures of the relative favourability of the respective environments.

The values of r_m (Tables 2 and 4) vary from 0.759 to 1.662 for temperature experiments and from 1.053 to 1.667 in radiation experiments, depending on temperature and radiation dosages given to the population. A higer r_m in a population does not necessarily mean that such a population will be more successful. The higher r_m for populations kept at 27°C may indicate that a rise in the innate capacity for increase can most readily be obtained by increase of the rate of egg production early in life (TANTAWY, 1961). A heterozygous individual such as AR/CH does not breed true, therefore r_m has no meaning except in the situation in which the population consists only of AR/CH.

Considering the mean generation length (Table 2) it is interesting to note that this character increases with decreasing temperature, and within the same temperature, particularily the higher one, there are significant differences ($P < 0.05$) between the different karyo-

TABLE 4

RATE OF INCREASE IN DIFFERENT IRRADIATED POPULATIONS

enotypes	Intrinsic rate of increase (r/day)	Mean generation length in weeks (T)	Net reproduction rate (R_0)	λ = Antilog$_e$ r_m
ontrols:				
AR/AR	1.401	2.47	31.72	5.06
AR/CH	1.373	2.71	41.14	3.33
CH/CH	1.471	2.06	20.63	4.36
500r				
AR/AR	1.402	2.48	32.42	4.06
AR/CH	1.383	2.61	36.88	3.97
AR/CH	1.234	2.82	32.62	3.42
CH/CH	1.677	1.75	18.81	5.37
AR/AR	1.434	2.42	31.99	4.18
AR/CH	1.243	2.72	29.40	3.46
CH/CH	1.304	2.17	17.04	3.67
000r				
AR/AR	1.439	2.23	24.85	4.22
AR/CH	1.347	2.48	28.24	3.86
AR/CH	1.342	2.43	26.07	3.82
CH/CH	1.466	1.74	12.76	4.35
AR/AR	1.270	2.33	19.24	3.56
AR/CH	1.317	2.40	23.49	3.74
HC/CH	1.437	1.81	13.53	4.22
500r				
AR/AR	1.282	1.95	12.14	3.60
AR/CH	1.263	2.40	20.77	3.52
AR/CH	1.163	2.57	20.04	3.19
CH/CH	1.274	1.57	7.41	3.56
AR/AR	1.245	1.92	10.96	3.46
AR/CH	1.161	2.43	16.74	3.19
CH/CH	1.053	1.71	6.07	2.86

ypes. At 15°C and 25°C the heterozygous individuals live longer han either of the two homozygous groups. The situation is similar n radiation experiments where generation length declines with ncreasing dosages and in all cases heterozygotes live longer. The

results of Table 2 for 25°C indicate clearly that heterozygous populations would tend to increase in number more rapidly than homozygotes. At 15°C the carrier of the AR/AR gene arrangement may tend to increase faster than the carriers of AR/CH and CH/CH, while at higher temperature the situation is reversed in favour of CH/CH gene arrangements. These findings are in general agreement with those reported by WRIGHT & DOBZHANSKY (1946) whose work suggested that r_m in *Drosophila pseudoobscura* populations is a function of the different inversions in the third chromosome. BIRCH (1960) stated that species differ genetically in the capacity to increase in number, and "natural selection would tend to maximize r_m for the environment in which a species lives, for any mutation or gene combination which increases the chance of genotypes possessing them contributing more individuals to the next generation (that is of increasing r_m) will be selected over genotypes contributing fewer of their kind to successive generations. This is the usual meaning of fitness of genotype. The tendency of natural selection to maximize r_m does not necessarily mean that natural selection will tend to make the number of species a maximum".

The fact that the intrinsic growth rate has not before been reported in *Drosophila* species and the results of the present studies raise a problem which should be investigated on natural populations of *Drosophila* captured from different geographical regions. Such a problem will be taken into consideration in future experiments.

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10. Studies on natural populations of Drosophila.
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STUDIES ON NATURAL POPULATIONS OF *DROSOPHILA*. I. HEAT RESISTANCE AND GEOGRAPHICAL VARIATION IN *DROSOPHILA MELANOGASTER* AND *D. SIMULANS*

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Under laboratory conditions quantitative characters in *Drosophila*, such as body size or fecundity, are very sensitive to environmental changes, e.g., temperature fluctuations or changes in quality or quantity of food. In nature, the same situation is found where changes in annual temperature or humidity affect the type of flora as well as the size of *Drosophila* fauna.

It is well known that there is a correlation between some quantitative characters and the geographical distribution of animals. Thus, the pioneer work of Timofeeff-Ressovsky (1933) showed that strains of *Drosophila funebris* and *Drosophila melanogaster* derived from different geographical regions react differently to temperature. Studies on the morphology of wild populations as those reported by Dobzhansky (1937), Reed and Reed (1947) on *Drosophila pseudoobscura* and *Drosophila persimilis*, Stalker and Carson (1947, 1948 and 1949) on *Drosophila robusta*, Prevosti (1955) on *Drosophila subobscura*, demonstrated that wing length and other traits decrease in size with geographical distribution from north to south.

The early work of Dobzhansky and his collaborators showed that natural populations of *Drosophila pseudoobscura* in different geographical localities differed in the frequency of various inversions in the third chromosome. Further work by Dobzhansky revealed that within one locality, populations of *Drosophila pseudoobscura* exhibited seasonal variations in respect to the frequency of different inversions.

Laboratory investigations designed to test the reaction of various gene arrangements to different temperature conditions have been carried out by Dobzhansky in a series of papers on *Drosophila pseudoobscura*, Kalmus (1945) on *Drosophila melanogaster*, Dubinin and Tiniakov (1945) on *Drosophila funebris*, Moos (1955) and others on *Drosophila pseudoobscura*, and Spiess (1958) on *Drosophila persimilis*. They all found that various genotypes react differently to various temperatures.

The present study, the first of a projected series dealing with natural populations of *Drosophila* in the Middle East and surrounding areas, was designed to test an hypothesis concerning the nature of developmental homeostasis. The hypothesis to be tested can be expressed as follows: progeny

FIG. 1. Different geographical regions from which populations of *Drosophila melanogaster* and *Drosophila simulans* were captured.

of euryokous populations (i.e., populations that have a wide tolerance for various environmental factors) are better able to withstand the upper and lower limits of experimental laboratory conditions than progeny of stenokous populations.

TECHNICAL PROCEDURE

Collecting technique. All collections of *Drosophila* in the present investigation and in the future, have been and will be carried out by exposing cans measuring 6×8 in., each containing one pound of ripe bananas which was mashed, autoclaved, and then inoculated with a suspension of baker's yeast. At the time of collection, i.e., in the early morning and late afternoon, Dobzhansky and Epling (1944), about a dozen of these cans were placed on the ground in the shade of trees to attract the flies. The *Drosophila* were collected with the aid of collecting nets and were then transferred into vials containing cornmeal-molasses-agar medium.

In the laboratory the flies were etherized. Males of *Drosophila melanogaster* and *Drosophila simulans* were classified as to species by examining the genitalia. Females were placed in individual culture bottles and classified by examination of their male progeny.

Localities. Natural populations of *Drosophila melanogaster* and *Drosophila simulans* were sampled from several localities, as shown in figure 1, one each from Lebanon (Safa Valley, 3,500 ft altitude) Uganda (Namulonge, 3,775 ft altitude) and three populations from Egypt (approximately at sea level). The Egyptian populations were captured from: the University of Alexandria Farm, Alexandria; Wadi-El-Natroon, an isolated desert area halfway between Alexandria and Cairo (92 km southwest of Cairo); Luxor, about 550 km south of Cairo. *Drosophila melanogaster* as well as *Drosophila simulans* were found in all these localities except Luxor, where only *Drosophila melanogaster* was found. However a *simulans* population from Beni-Swef, about 112 km south of Cairo, was substituted for this one. These localities are designated as: LB, UG, UF, WD, LX, and BS, respectively.

Most of the collecting was done during July and August in 1956, by placing the cans under grape vines, fig, or palm trees. Dobzhansky et al. (1957) did a preliminary survey collection of the *Drosophila* fauna in

TABLE 1. *Monthly averages of percentages of humidity and temperature in different geographical regions in 1956*

Locality	Humidity %	Temperature ° C
LB	60.21 ± 8.91	16.15 ± 7.38
UF	69.17 ± 7.02	20.04 ± 6.35
WD	63.66 ± 12.52	21.55 ± 6.95
BS	54.83 ± 15.24	21.90 ± 7.30
LX*	29.12 ± 14.05	25.49 ± 9.52
UG	72.94 ± 2.95	27.34 ± 1.34

* % humidity and temperature were not recorded from September to December.

Egypt and obtained the frequency distribution of adults of *Drosophila melanogaster* and *Drosophila simulans* captured from the above mentioned regions as well as other localities in Egypt. Average percentages of humidity and temperatures recorded in 1956 for all localities are presented in table 1, indicating that the Uganda locality shows the highest percentage of humidity and temperature which are constant through the year, and that the Lebanon locality is the coldest, with wider fluctuations.

Experimental. Ten captured fertilized females each of *Drosophila melanogaster* and of *Drosophila simulans* were chosen at random from each locality and placed in separate culture bottles for two days, and then transferred into fresh bottles every other day for a week in order to establish the original foundation populations. At every generation, the offspring of the ten females from each locality were intercrossed to obtain ten new bottles. In other words, males from the first bottle were intercrossed with virgin females of the second bottle, males from the second bottle with females of the third bottle, and so on to produce the first and second new bottles, respectively. Such a procedure was made to obtain the first nine bottles. The tenth new bottle was obtained by intercrossing males of the first bottle with virgin females of the tenth bottle. Progeny of the first generations of these females were not used in order to avoid any possible influence of the original environmental conditions in which females had survived.

The five different populations of *Drosophila melanogaster* and of *Drosophila simulans* were exposed to the following temperatures: 10°, 15°, 18°, 22°, 25°, 28°, 30°, and 31° C. Populations of *Drosophila melanogaster* were examined also at 31.5° C and those of *Drosophila simulans* at 30.5° C (the upper limits of temperature at which progeny can be obtained in these species). These temperatures were held constant to within 0.1° C.

Within a given temperature and locality virgin females from each of the bottles were intercrossed with males from other bottles to maintain the foundation stock as heterozygous as possible. Samples of flies were taken at random from each bottle (20 pairs) and were placed in oviposition bottles; thus one hundred oviposition bottles were used for all the populations at a given temperature. Eggs were collected from these bottles at a known temperature and cultured at the same temperature.

From each of the oviposition bottles samples of eggs were obtained and cultured in five food vials. To prevent competition in the larval stage not more than seventy eggs were introduced into each vial which contained the normal food culture. Collection and culturing of eggs were carried out on four successive days and after emergence adults were counted and classified as to sex.

From the populations emerging from each of the two vials during the first two days, ten males and ten females were obtained at random on each day, in order to measure wing and thorax length. Thus a total of 400 males and females from each locality in each temperature were examined. The total number of flies emerging from all vials on the four days was used to get an estimate of the percentage of emergence and sex-ratio in the progeny.

Measurements of wing and thorax length were obtained by the method described by Robertson and Reeve (1952) and used by the senior author as described in previous publications, Tantawy (1959). At a given temperature, all populations were treated at the same time in the same manner and to minimize environmental fluctuations the methods recommended by Robertson and Reeve were used.

Results and Discussion

Wing and thorax length. It was known from the work of Mellanby (1954) that some insects can become acclimatized to changes in temperature. Smith (1957) found that in individuals of *Drosophila subobscura* acclimatization takes place and depends on whether animals are homozygous or heterozygous, the latter showing more acclimatization.

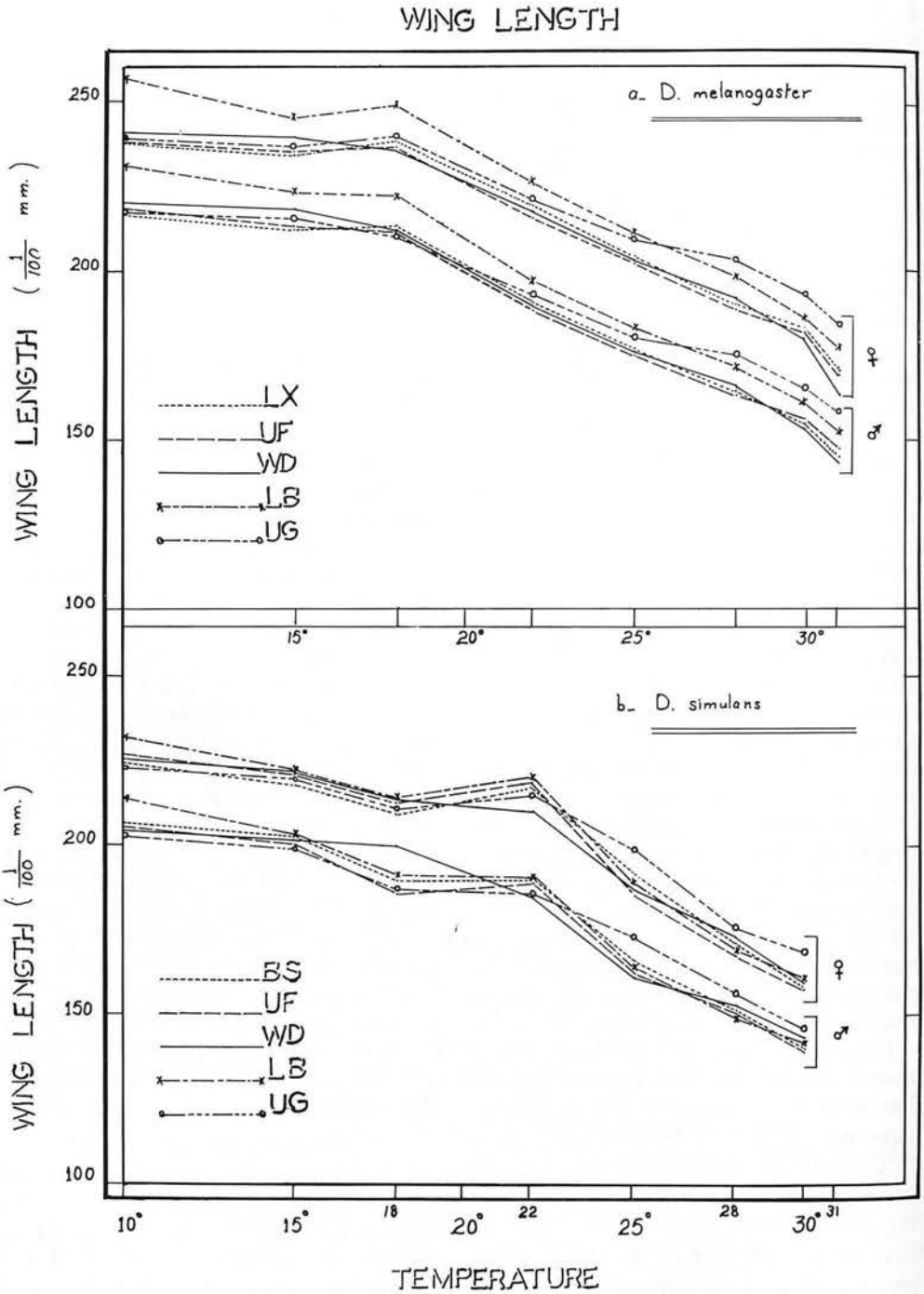


FIG. 2. Wing length in *Drosophila melanogaster* and *Drosophila simulans* at various temperatures. Units of measurement are 1/100 mm.

Our results secured from the present experiment on the effects of various degrees of temperature on body size, i.e., wing and thorax length, in *Drosophila melanogaster* and *Drosophila simulans* are presented in figure 2 a and b for both species, respectively. Results obtained for thorax length are not given since they show a similar pattern of behavior as that obtained in the wing length.

The results as presented in figure 2 a and b indicate clearly that *Drosophila melanogaster* is significantly larger in wing length at any given temperature than is *Drosophila simulans*, and in both species the females are larger than the males. Various degrees of temperature show highly significant effects on body size; wing length is longer at the lower temperatures and decreases gradually with the increase of temperature. The average percentage of decrease, for both sexes in all populations of *Drosophila melanogaster*, from the lowest to the highest degrees, is 31.03 per cent and 18.66 per cent for wing and thorax length, respectively, and 31.79 per cent and 22.89 per cent in *Drosophila simulans* for both dimensions, respectively. Such results indicate that although *Drosophila melanogaster* is bigger in size than *Drosophila simulans*, both species were affected similarly by temperature changes, especially in regard to wing length. Such a phenomenon of changing wing length with various degrees of temperature are in agreement with the results of Stalker and Carson (1947) working on *Drosophila robusta* and Pantellouris (1957) on *Drosophila melanogaster*.

Considering the different populations from the various geographical regions, the results indicate that in both species populations from Lebanon are larger in wing length than other populations, at almost every temperature. Such a population is morphologically larger than that from Uganda where the lower temperature prevails, but the situation is reversed at the higher temperatures, where UG populations show superiority in size to all other populations. Other populations captured from Egypt do not show any significant differences between them and showed almost the same size as UG populations, except at the higher temperatures where the latter ones show longer wing length. These results will be discussed later.

Thorax length of all populations behaved almost in the same manner as wing length and figure 3 a and b for *Drosophila melanogaster* and *Drosophila simulans* shows a highly positive correlation between the two measurements. The results are presented as log of wing plotted against log of thorax which indicate also that wing length is affected more than thorax length, particularly at the extreme temperatures. Such a point can be illustrated more clearly when measurements for both dimensions are expressed as a ratio of wing/thorax length. The results for wing/thorax ratio in *Drosophila melanogaster* and *D. simulans* indicate that with an increasingly cold climate, wing length is longer relative to thorax length than it is at higher temperatures, a fact which agrees fairly well with the findings of Stalker and Carson (1947) and Pantellouris (1957). It has also been shown by Reeve and Robertson (1953) that changes of temperature during the pupal stage may have profound effects on wing length but not on thorax length.

Phenotypic variance. Phenotypic variance of wing length is expressed as the coefficient of variation and the results are presented in figure 4 a and b for *Drosophila melanogaster* and *D. simulans*.

The results as presented in figure 4 indicate that temperature has a highly significant effect on variability of wing length in all populations studied. Such variation is high at the two extremes of the temperature; higher temperatures show more effects on phenotypic variation than lower or intermediate ones. The smallest coefficients of variation appear when flies were exposed to intermediate temperatures. The results also indicate that UG populations are the highest in phenotypic variance at almost every temperature, but are the lowest at the highest temperatures. LB populations show more

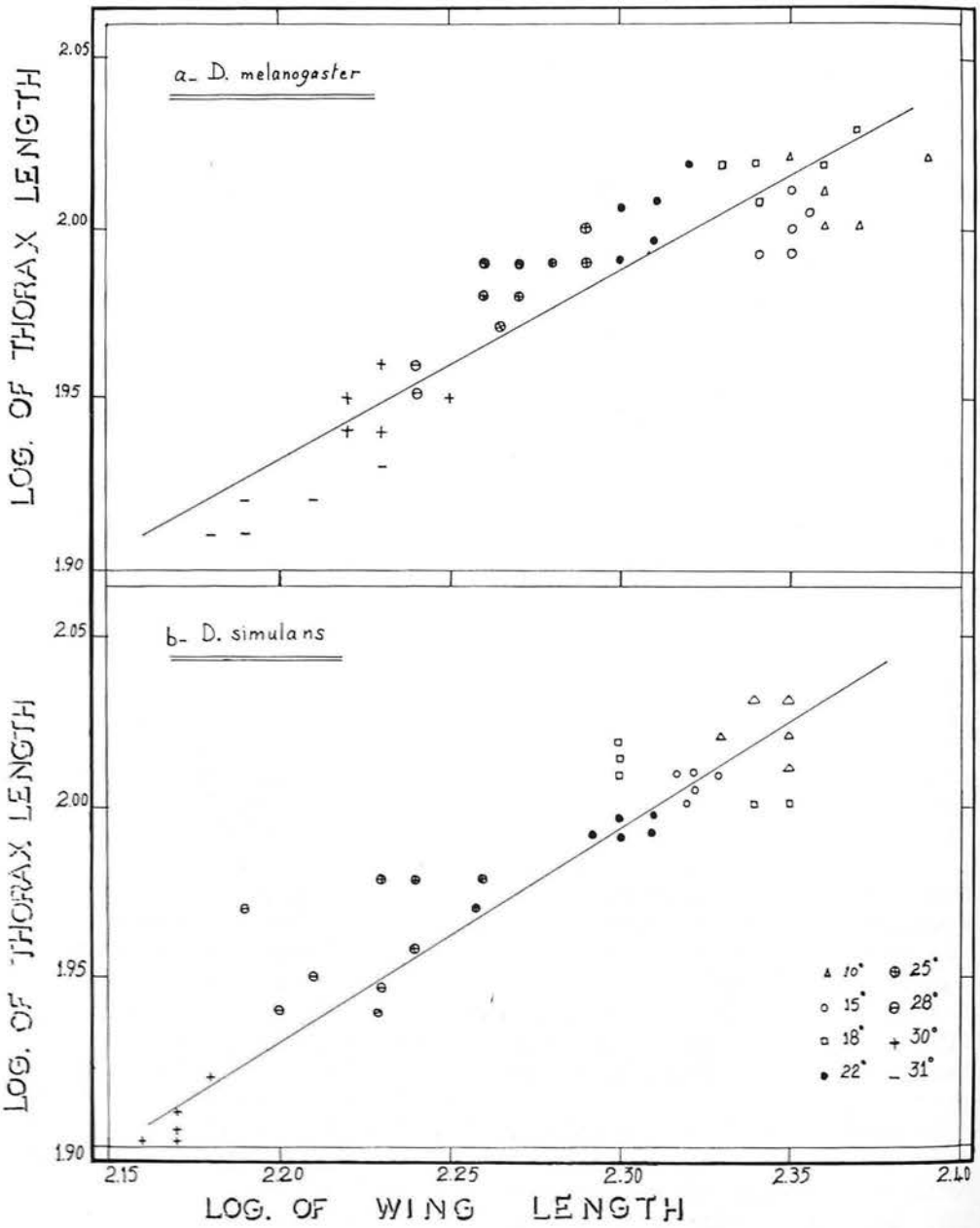


FIG. 3. Log of wing length plotted against log of thorax length in all populations of *Drosophila melanogaster* and *Drosophila simulans*.

uniformity in wing length than other populations but become the most variable at the highest temperature.

Such differences in phenotypic variance will be discussed later, but it would be of great interest to know whether the variance is a reflection of different responses of similar genotypes, or whether it is a reflection of

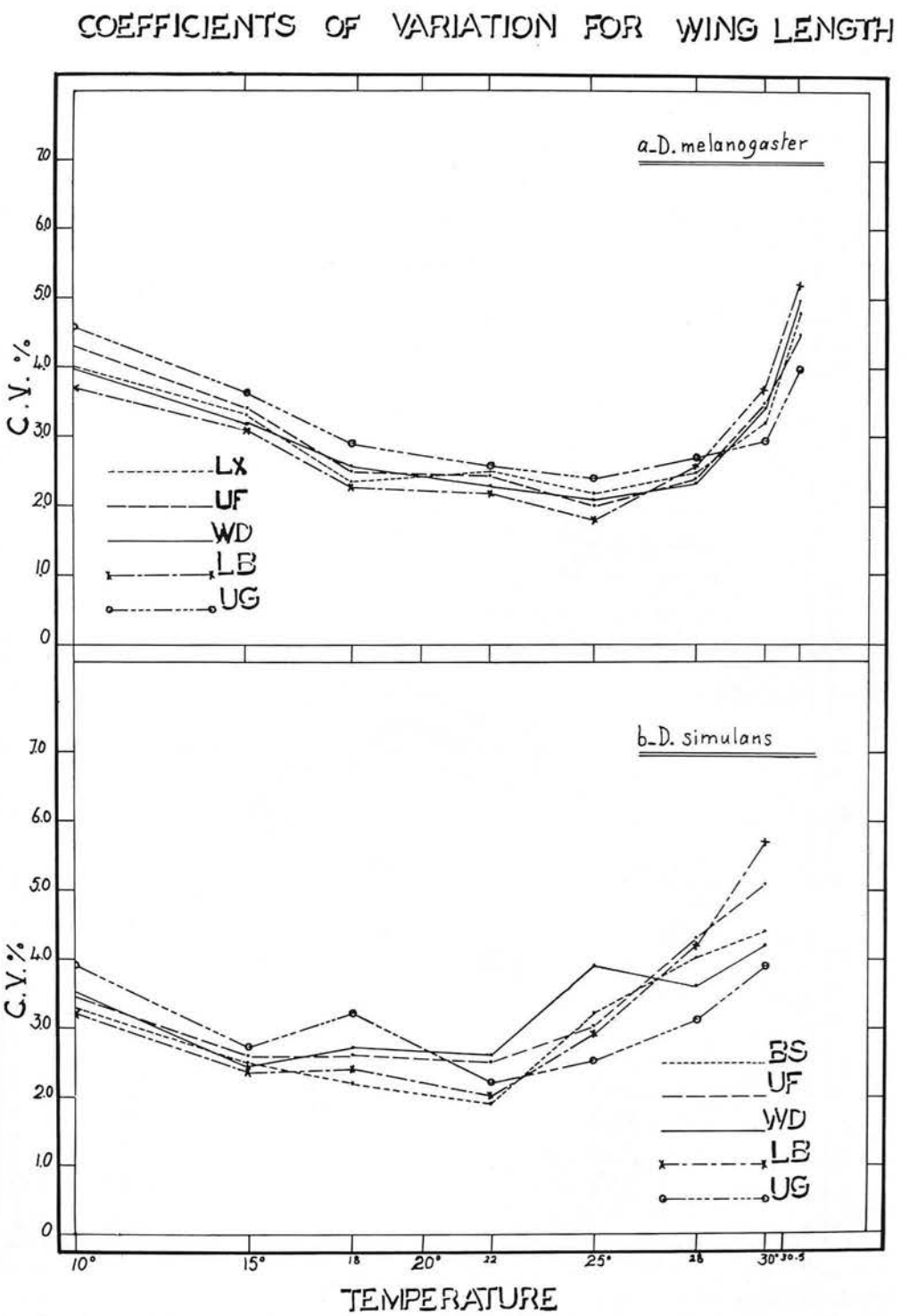


FIG. 4. Coefficients of variation for wing length of all populations of *Drosophila* in respect to different degrees of temperature.

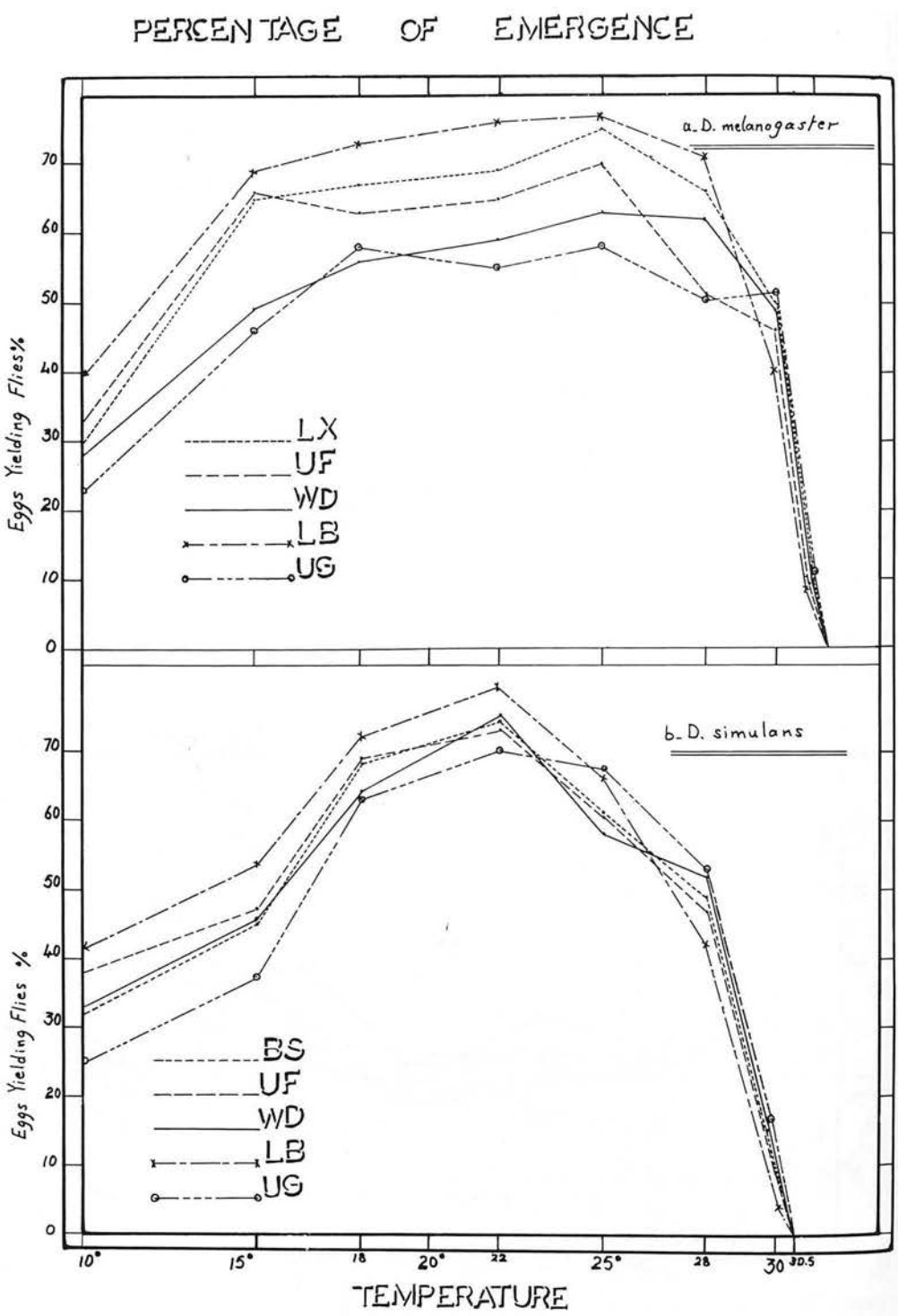


FIG. 5. Percentage of emergence in all populations of *Drosophila*.

a wider range of genotype within a given population. This point we hope to investigate in the near future.

Percentage of emergence. Percentage of emergence is measured by the number of adult flies that hatched from a certain number of eggs cultured in food vials. The results obtained are presented in figure 5 a and b for *Drosophila melanogaster* and *D. simulans*.

The results as shown in figure 5 demonstrate that different temperatures have various effects on the percentage of emergence. In all the populations studied the percentage of emergence is about 25–40 per cent at the lowest temperature, increasing gradually with the increase of temperature. The maximum percentage of emergence can be seen at 25° C, i.e., 58–76 per cent in *Drosophila melanogaster* and at 22° C, i.e., 69–79 per cent in *D. simulans*, which shows that optimal conditions for both species may be different. At higher temperatures, the percentage of emergence decreases gradually to 8 per cent and 5 per cent in both species. Complete lethality of pupae occurs at 31.5° C in *Drosophila melanogaster* and 30.5° C in *D. simulans*, thus showing a temperature difference between these sibling species.

Populations from the extreme north and extreme south end of the range differ in their per cent emergence in the same way as they differ in wing length. Populations from LB show higher percentage of emergence at almost every temperature, except that at highest temperatures where UG populations show the best viability.

If we plot percentage of emergence against the coefficients of variation for wing length the results demonstrate a highly significant negative correlation between such characters in both species. It is of interest to note that, at lower temperatures, LB populations are superior to UG populations where the former show a higher percentage of emergence and lower variation for wing length, but at the higher temperature the situation is reversed.

Optimal conditions and geographical distribution. There is extensive evidence on *Drosophila* species other than *Drosophila melanogaster* and *Drosophila simulans* which indicates that wing length shows an increase in northern geographical regions, e.g., Stalker and Carsons (1947, 1948 and 1949) on *Drosophila robusta*, Dobzhansky (1948) on *Drosophila pseudoobscura* and Prevosti (1955) on *Drosophila subobscura*.

Our results, summarized in figures 2, 4, and 5, suggest that the optimal temperatures for *D. melanogaster* and *D. simulans* are 25° C and 22° C, respectively. The values of the various characters studied at these optimal temperatures are shown in table 2, the localities being arranged in north to south order.

The results thus presented in table 2 indicate that northern populations, i.e., LB, are significantly larger in size, less variable and more viable than those from the extreme south, i.e., UG populations. In *D. simulans* there is a gradient of size from north to south, while in *D. melanogaster* flies from central Egypt are the smallest. Such differences in behavior and the insignificant differences between some of the Egyptian populations and that from Uganda could be explained on the basis of possible immigration throughout the Nile Valley. LB populations are isolated from the Egyptian ones by the Sinai Desert. If we consider LB populations as northern populations and all other populations, i.e., from Egypt and Uganda, as southern ones, we find significant differences between them in every respect; the former populations are larger, less variable and more viable than the latter ones, which agrees well with the findings of other investigators.

It seems probable, therefore, from such results, that the geographical differences in morphology are the results of an adaptation to climate and such adaptation may be of indirect effect. Dobzhansky (1937) stated that the morphological phenotype may be the by-product of some more fundamental physiological adaptation. Annual mean temperature as well as percentage humidity are the more obvious environmental conditions, which show correlations with the

TABLE 2. *Morphological differences between males and females of* Drosophila melanogaster *and* Drosophila simulans *in mean wing and thorax length, at their optimal temperatures, with their respective coefficients of variation (C.V.%). Units of measurement are 1/100 mm. Percentages of emergence are also presented.*

Population	Wing Length*				Thorax Length*				Percentage of emergence
	Males		Females		Males		Females		
	Size	C.V.	Size	C.V.	Size	C.V.	Size	C.V.	
Drosophila melanogaster									
LB	183.41	1.86	211.09	1.70	93.69	2.40	106.11	2.19	76.18
UF	175.59	1.97	203.19	2.11	89.48	2.59	102.39	2.19	68.70
WD	176.10	2.29	202.60	1.97	91.40	3.37	104.74	2.45	63.13
LX	176.16	2.36	203.78	1.99	90.81	2.64	103.87	2.22	73.89
UG	180.03	2.50	210.27	2.36	91.54	3.41	105.03	2.57	58.11
Drosophila simulans									
LB	190.91	2.17	220.16	1.87	95.63	2.96	109.95	2.36	79.91
UF	189.36	2.77	218.66	2.19	94.75	2.84	108.39	2.27	72.59
WD	184.97	2.73	209.63	2.49	91.20	3.52	104.54	3.03	74.84
BS	189.44	2.25	217.98	1.79	94.81	2.86	108.86	2.66	74.83
UG	185.96	2.58	215.52	1.99	92.41	3.21	107.31	2.47	69.49

* Each mean is taken from 200 pairs of adult flies.

phenotypic appearance of the animal. Other environmental conditions such as type of flora may have some effects on such adaptation. In sum, we find that animals which are adapted to a given temperature are less phenotypically variable than those not adapted.

Sex-ratio. It is a known fact that wild populations of *Drosophila* give a sex-ratio almost of 1:1 under optimal conditions. When environmental conditions are changed the ratio is also changed.

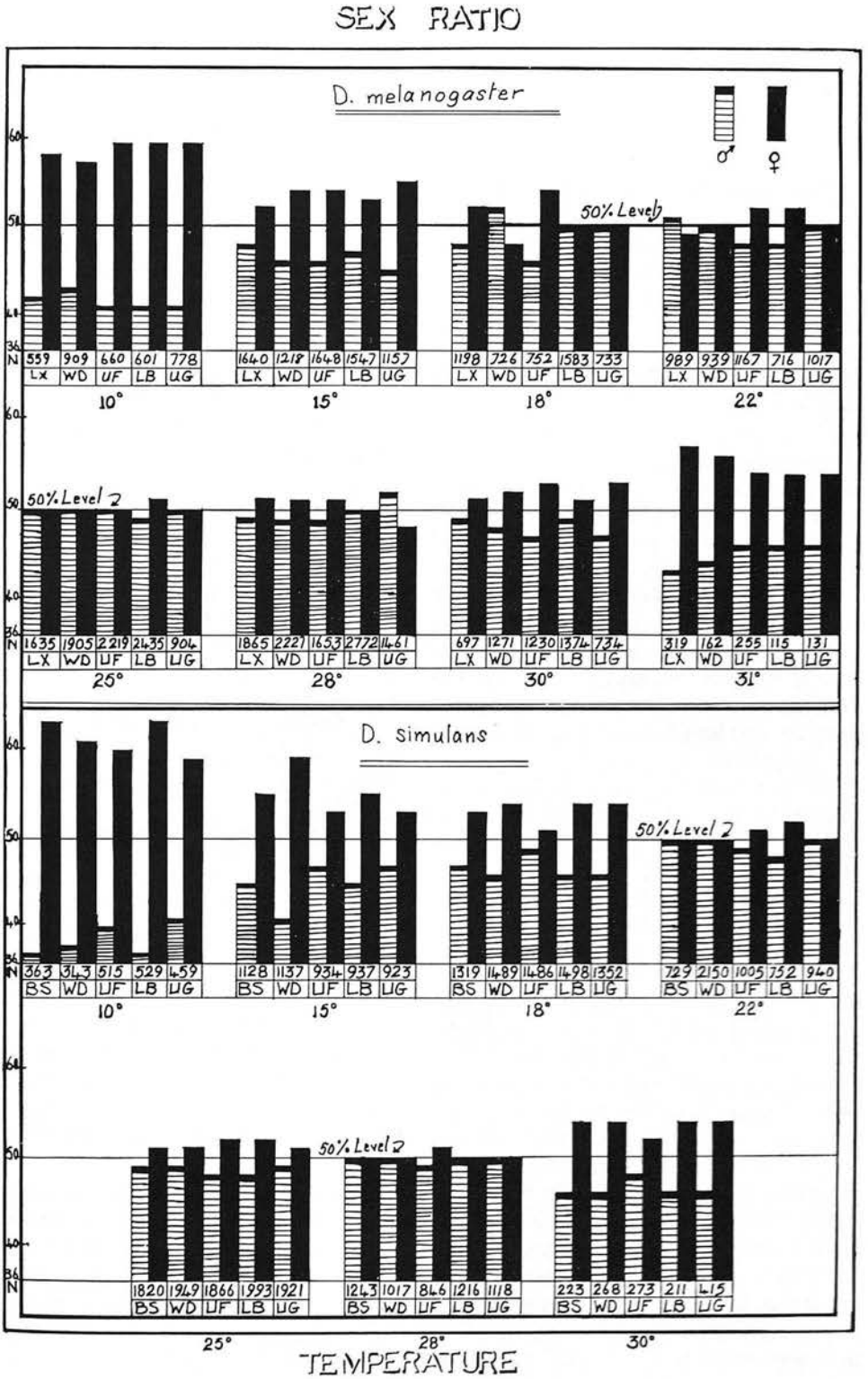
There are some exceptional situations reported in which some wild-type females captured from nature give rise to a highly abnormal sex-ratio. Thus, Magni (1954), Moriwaki et al. (1957) working on *Drosophila bijasciata*, Cavalcanti and Falcau (1954) on *D. prosultans*, Stalker (1957) on *D. paramelanica* and Malogolowkin et al. (1959) on *D. willistoni*, all reported abnormal sex-ratio arising from some wild females. Malogolowkin et al. (1959) attributed such an abnormal situation to the action of an agent which is transmitted by the female to all her eggs and is lethal in XY zygote.

In the present investigation, all hatched flies were classified to sex and the results for the various sex-ratios at the different temperatures are presented in figure 6 a and b for *Drosophila melanogaster* and *D. simulans*, where locality and total number of adults counted are also shown.

The results as shown in figure 6 indicate an influence of temperature on sex-ratio. At lower and higher temperatures in both species there are significant differences between sexes; females predominate, while at milder temperatures the ratio is almost one to one. During the experiment it was noticed that at the two extremes of temperature, particularly at the higher one, pupae fail to develop into adults. It was observed that adults attempted to emerge from the pupae, but only succeeded in dragging their heads and thorax out of the pupal case.

One may conclude from these results, that females are the stronger sex in resisting

FIG. 6. Sex-ratio for all populations of *Drosophila* under various degrees of temperature; populations and number of adults counted in each locality are also illustrated.


SEX RATIO
D. melanogaster
♂
♀
Sex ratio %
50% Level
N
559 909 660 601 778
LX WD UF LB UG
10°
1640 1218 1648 1547 1157
LX WD UF LB UG
15°
1198 726 752 1583 733
LX WD UF LB UG
18°
989 939 1167 716 1017
LX WD UF LB UG
22°
50% Level
1635 1905 2219 2435 904
LX WD UF LB UG
25°
1865 2227 1653 2772 1461
LX WD UF LB UG
28°
697 1271 1230 1374 734
LX WD UF LB UG
30°
319 162 255 115 131
LX WD UF LB UG
31°
D. simulans
Sex ratio %
50% Level
363 343 515 529 459
BS WD UF LB UG
10°
1128 1137 934 937 923
BS WD UF LB UG
15°
1319 1489 1486 1498 1352
BS WD UF LB UG
18°
729 2150 1005 752 940
BS WD UF LB UG
22°
Sex ratio %
50% Level
1820 1949 1866 1993 1921
BS WD UF LB UG
25°
1243 1017 846 1216 1118
BS WD UF LB UG
28°
223 268 273 211 415
BS WD UF LB UG
30°
TEMPERATURE

changes in temperatures and are also better buffered than males. Such resistance became apparent in the immature stages of adults, particularly in the pupal stage.

Conclusions

The earliest studies of geographical variation in different species of *Drosophila* have been reviewed by Stalker and Carson (1947). It has been found that size of an animal differs according to altitude and northern animals are larger in size than southern ones.

Our results as reported, show clearly that body size and percentage of emergence as well as sex-ratio can be altered by changing temperature conditions; the latter two characters are the more sensitive ones. Such alteration in the new laboratory conditions depends to a great extent on the original climatic conditions in which flies had survived. Thus, LB populations of *Drosophila melanogaster* and *Drosophila simulans* are well adapted to the colder and milder degrees of temperature and UG populations to the warmer ones. Such populations are larger in wing length and thorax length with low phenotypic variances and higher viability under their adapted conditions. These findings are in general agreement with those of Lerner (1954) who stated that the poorest adapted individuals have higher variability. Since variability is usually regarded as a measure of homeostasis, on the assumption that a less variable phenotype indicates superior homeostatic buffering properties which result in a high general adaptedness in a range of environments, one may conclude that LB populations which are euryokous populations are more adapted to wider changes in environmental conditions than that of UG populations which are stenokous populations. An analysis of the geographical distribution of the two populations, shows that LB populations inhabit regions characterized by medium summer temperature and colder winter with a lower percentage of humidity, while UG populations were captured from a region where the temperature is 27° C almost constant throughout the year with a higher degree of humidity. Thus indicating that stenokous populations are better adapted only to a temperature similar to that of their native conditions. This is expected since natural selection acts more strongly on the euryokous populations than on the stenokous ones, therefore the former populations are able to adapt themselves to wider alterations of climatic conditions, i.e., they are more homeostatic. Results obtained in the present investigation are in agreement with those reported by Lewontin (1956 and 1957) who has equated homeostasis with fitness, which indicate that the physiological and morphological responses of a homeostatic individual are adaptive so as to favor survival.

The reaction of LB and UG populations to the temperatures, showing different adaptation to the extremes, gives rise to the following questions:

1. What would be the response to selection in populations of both localities under optimal conditions as well as colder and warmer temperatures?
2. Do crosses between and within different populations, under the previously mentioned conditions, yield the same degree of heterosis?

Such points will be investigated in future experiments.

Summary

1. Natural populations of *Drosophila melanogaster* and *Drosophila simulans* were captured from different geographical regions in Lebanon, Egypt, and Uganda.

2. Offspring of such populations were reared under different temperatures ranging from 10° to 31.5° C in *Drosophila melanogaster* and to 30.5° C in *Drosophila simulans*.

3. Wing and thorax length are greater at lower temperatures, decreasing gradually with increasing temperature, while the percentage of emergence is lower at the two extremes of temperature and significantly higher at optimal conditions.

4. Wing/thorax ratio is about 2 under

optimal conditions, increasing at lower temperatures and decreasing at higher ones.

5. Phenotypic variance of wing length is higher at both extremes, and much higher at warmer temperatures.

6. Complete sterility, i.e., eggs failing to produce adults, occurs at 31.5° C in all populations of *Drosophila melanogaster* and at 30.5° C in *Drosophila simulans*.

7. Lebanon populations, i.e., northern populations, are more vigorous, less variable and more viable than all other populations studied at almost every temperature, while populations from Uganda show superiority to all other populations only at the higher temperatures, i.e., their original climatic conditions.

8. Extremes of temperature adversely affect sex-ratio. At the two extremes of temperature females appear to be the stronger sex and are significantly more numerous than males. At milder temperature the sexes occur in equal numbers.

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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 direction) 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.%)*

	D. melanogaster				*D. simulans*			
	Wing length		Thorax length		Wing length		Thorax length	
Temperature	Mean	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
Males								
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
Females								
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 h^2	18°C No. of matings	24°C h^2	24°C No. of matings	28°C h^2	28°C No. of matings
a. *D. melanogaster*							
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. *D. simulans*							
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. simulnas*.

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

	D. melanogaster			*D. simulans*		
Progeny No.	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

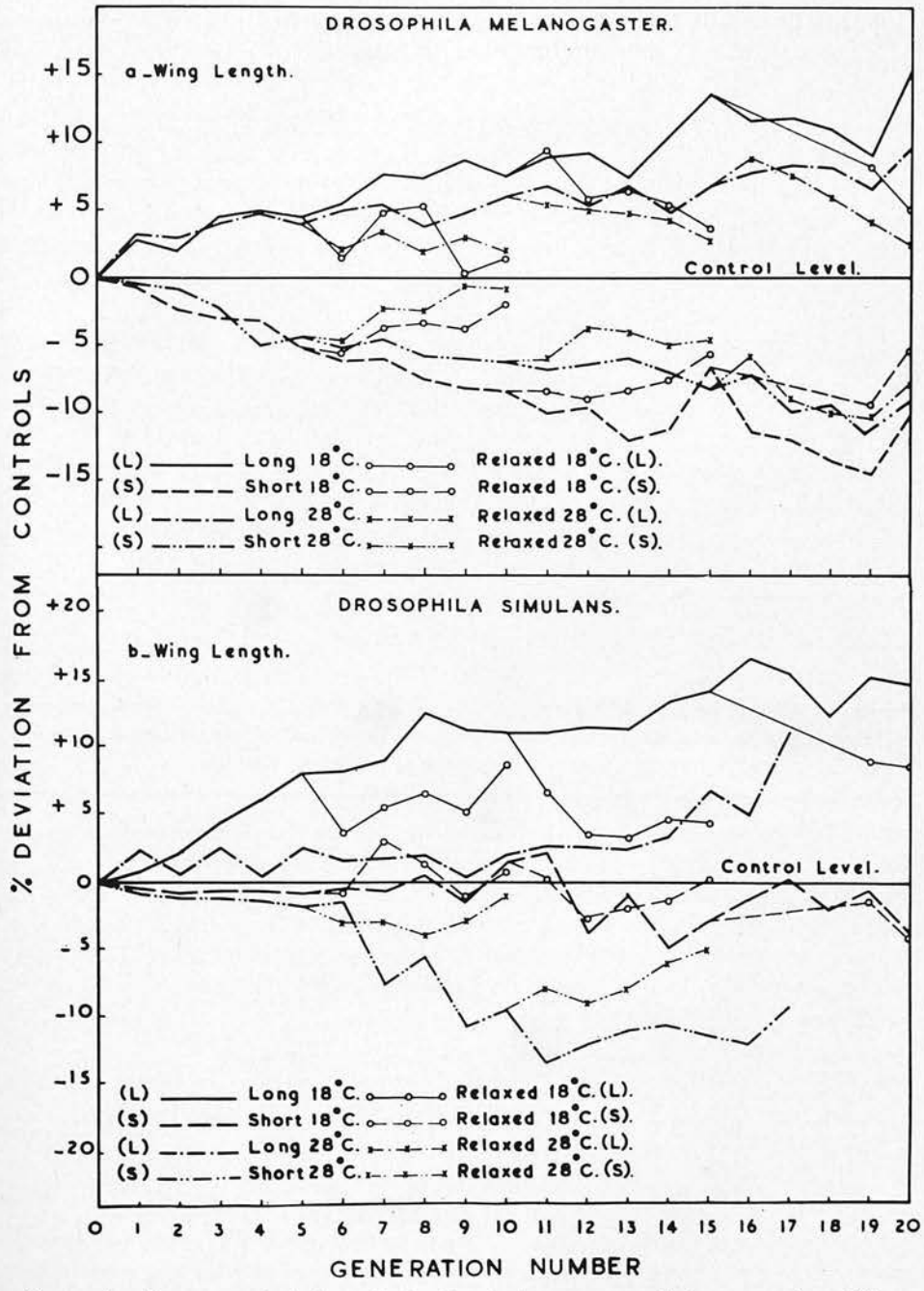

FIGURE 1.—Percentage deviations of wing length (sexes averaged) from controls at different temperatures.

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
a. *D. melanogaster*						
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. *D. simulans*						
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-

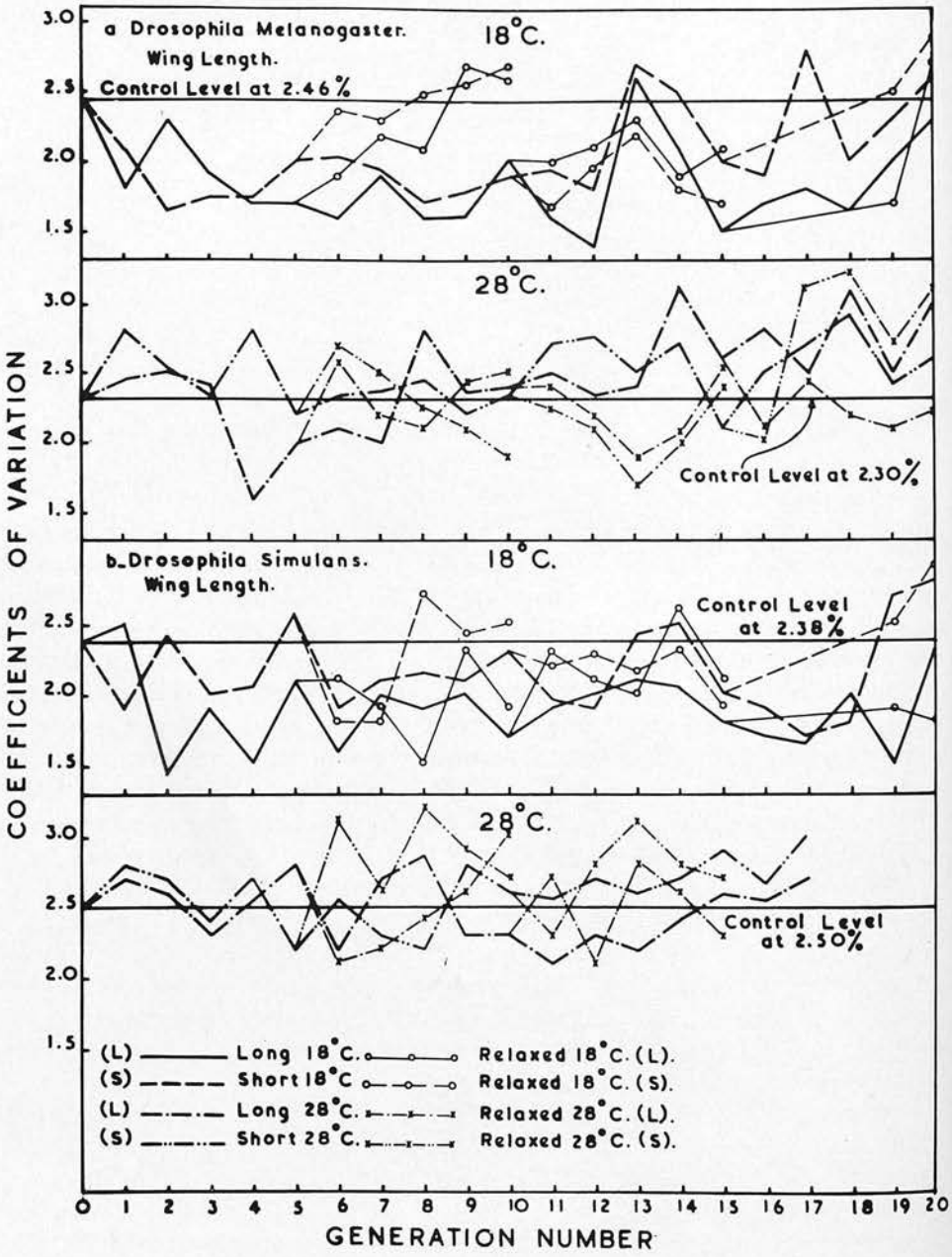

FIGURE 2.—Coefficients of variation for wing length (sexes averaged) at different temperatures.

TABLE 5

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

Generation	18°C		28°C	
	Long	Short	Long	Short
a. *D. melanogaster*				
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. *D. simulans*				
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
a. *D. melanogaster*				
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. *D. simulans*				
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
a. *D. melanogaster*				
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. *D. simulans*				
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-

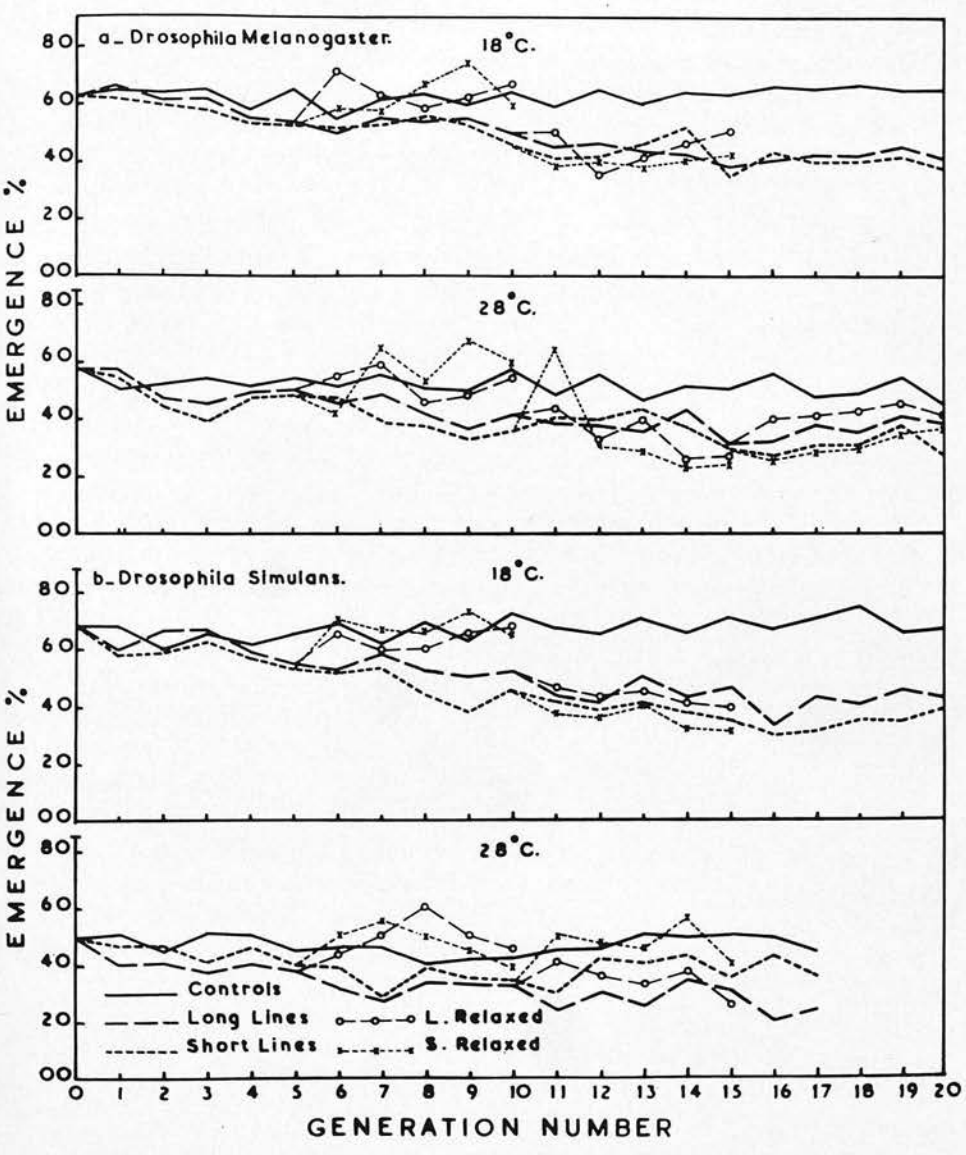

FIGURE 3.—Percentage of emergence (eggs to adults) in the selected lines at different temperatures.

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.

The authors are very indebted to DR. FORBES W. ROBERTSON of the Institute of Animal Genetics, Edinburgh, Scotland, for his helpful discussions and suggestions in the preparation of the manuscript.

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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12. Studies on natural populations of Drosophila. III. Morphological and genetical differences in wing length of Drosophila melanogaster and D. simulans in relation to seasonal fluctuations. Evolution, 18, In press (1964).

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June 22, 1964

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Dear Dr. Tantawy:

Your manuscript entitled "Studies on Natural Populations of Drosophila III" has come back to me and is hereby accepted for publication in Evolution. I will send it on to the managing editor within a few days and I expect that it will be published within six months.

Yours sincerely,

Charles D. Michener

Charles D. Michener
Editor

CDM:jka

Studies on natural populations of Drosophila. III. Morphological and genetical differences in wing length of Drosophila melanogaster and D. simulans in relation to seasonal fluctuations.

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One of the problems in the field of population genetics is the method to be used in investigating various factors affecting the genetic structure of a given population. Population density, temperature and humidity are among the important variables in studies the genetics and ecology of natural populations. Studies on genetically controlled morphological variation of metric characters in Drosophila have been reported by many authors. The results indicate that a population in a single locality may adapt itself to the cyclic climatic changes associated with season (for references see Tantawy and Mallah 1961).

A considerable amount of information has been gained through the analysis of the chromosomal gene arrangements

collection, identification of both species and technique used for tha maintenance of populations, see Tantawy and Mallah (1961).

2. Laboratory populations

Populations of the same two species captured in the same region five years perior to the experimental work were used. Populations of both species were kept by mass mating in breeding bottles at 25°C. under two different environmental conditions.

a. Optimal conditions, i.e. not more than 200 eggs from the mass mating population cultured in a well yeasted bottle.

b. Severe conditions of crowding, i.e. fifty pairs of flies per bottle were left to lay eggs freely in food bottles which were poorly yeasted.

These laboratory populations are called "optimal" and "severe" populations, respectively.

II. Experimental work

Two main experiments were carried out each month of the experimental period, to study the morphological and genetical differences in the various populations of Drosophila melanogaster and D. simulans.

1. Morphological differences

Progeny resulting from the F_2 generation of the

captured females in both species and those of the laboratory populations were used for collecting eggs to study the monthly morphological differences among various populations. For such a study, eggs from different populations were cultured monthly in well yeasted vials (not more than 50 eggs per vial) and after emergence of the adults, virgin females from each population and species, were obtained. Fifty males from each population were mated at random with fifty virgin females from the same population, in ten replicates; each one containing five pairs of flies. Flies were kept for feeding and mating for three days, after which they were transferred to oviposition vials for egg collection. Eggs from the various populations, laid on five successive days, were collected and cultured under optimal conditions (not more than 50 eggs per vial). After emergence, twenty pairs of flies from each vial, of each species and population, were measured for wing and thorax length. In all the matings, records were kept for the number of eggs cultured and the number of adults hatched.

2. Genetical differences

The following progeny tests were carried out for each species of Drosophila each month of the experimental period to study the monthly changes in the heritability estimates for wing and thorax length.

a. Fifty males captured in nature were used; each male being mated with three virgin females of the laboratory "optimal" condition population. The progeny tests were carried out under optimal conditions.

b. Fifty males from the laboratory "optimal" condition population were used, each male being mated with three virgin females of the same population. The progeny tests were carried out under optimal conditions.

c. Fifty males from the laboratory "severe" condition populations were mated, each with three virgin females of the same population. The progeny tests were carried out under severe conditions.

Other progeny tests from the laboratory "severe" condition populations were carried out during Autumn and Winter of 1962. Each month, fifty males from each species were used, each being mated with three virgin females of the same population, and the progeny tests were maintained under optimal conditions similar to those of (a) and (b) above.

In all the various progeny tests flies were measured for wing and thorax length before mating. Matings were made at random and the parents were kept in food vials for feeding and mating for five days, after which the three females in each mating were separated, each female being kept in a separate food vial. Eggs were counted daily from each female

and cultured in well yeasted vials for optimal conditions or with less food and yeast for severe ones.

After hatching, adults were counted and classified as to sex. Ten pairs of flies were measured for wing and thorax length from each vial on two successive days. Heritability estimates for both dimensions were calculated by the method of the half-sib analysis (Falconer 1960) on the basis of equal numbers of progeny per female.

All the experimental work in the present study were carried out at 25° ± 0.50°C.

Results

1. Morphological differences

a. Population density and sex-ratio in nature, in relation to temperature and humidity

Figure 1 represents mean daily temperature per month and the mean daily percentage of humidity throughout the experimental period. The data indicate that monthly temperature (average per day) declined from September 1961 to February, 1962 (25°C. to 12.5°C.) after which it increased gradually to August, 1962 when it was 27°C. Percentage of humidity behaved almost in a parallel fashion; the highest temperature and humidity were found during summer months.

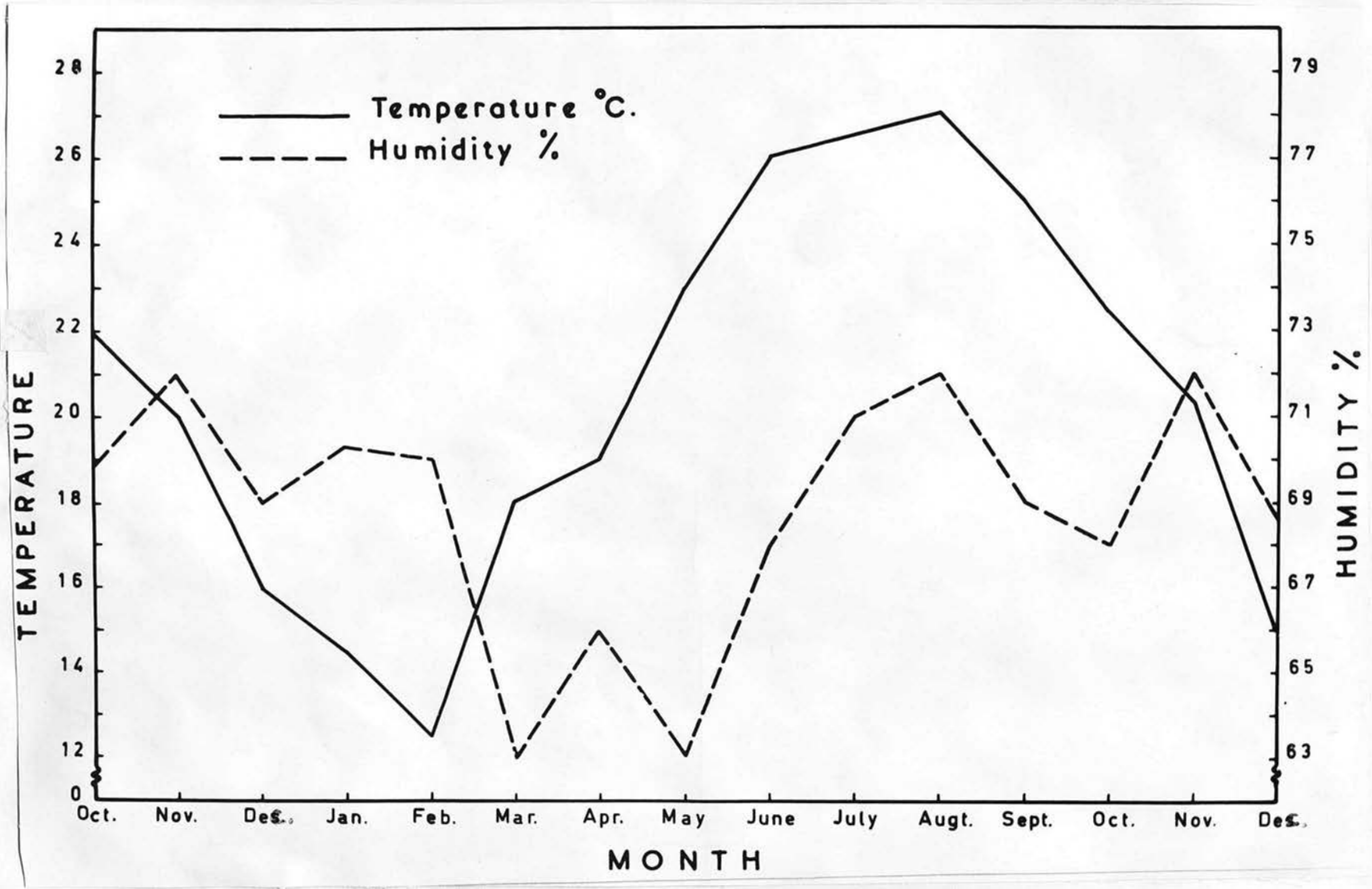

Figure 1. Daily average per month for temperature and percentage of humidity from October 1961 up to December 1962.

Figure 2 shows the total number of flies captured per month (both sexes) for Drosophila melanogaster and D. simulans. The number may reflect the abundance of the flies in nature, since the extensive monthly collections were made twice a month in the same locality of approximately one square mile using thirty traps every time (Tantawy and Mallah 1961).

Figure 2 also shows that the highest peaks for the number of captured flies were during the period from July to October. One of the interesting points seen in Figure 2 is the excess of Drosophila simulans over D. melanogaster during October and November of both years.

Sex-ratio presented as percentage of males in the captured flies of both species of Drosophila is given in table 1. The results indicate that females are captured in excess through the whole period. A decline of males (shown by significant χ^2 tests) during summer months is shown in table 1.

These results indicate that females can resist high temperature better than males, supporting the results given by Tantawy and Mallah (1961) working on the same two species of Drosophila. Sex-ratio in the laboratory populations is nearly 1 : 1 though females exceed males slightly.

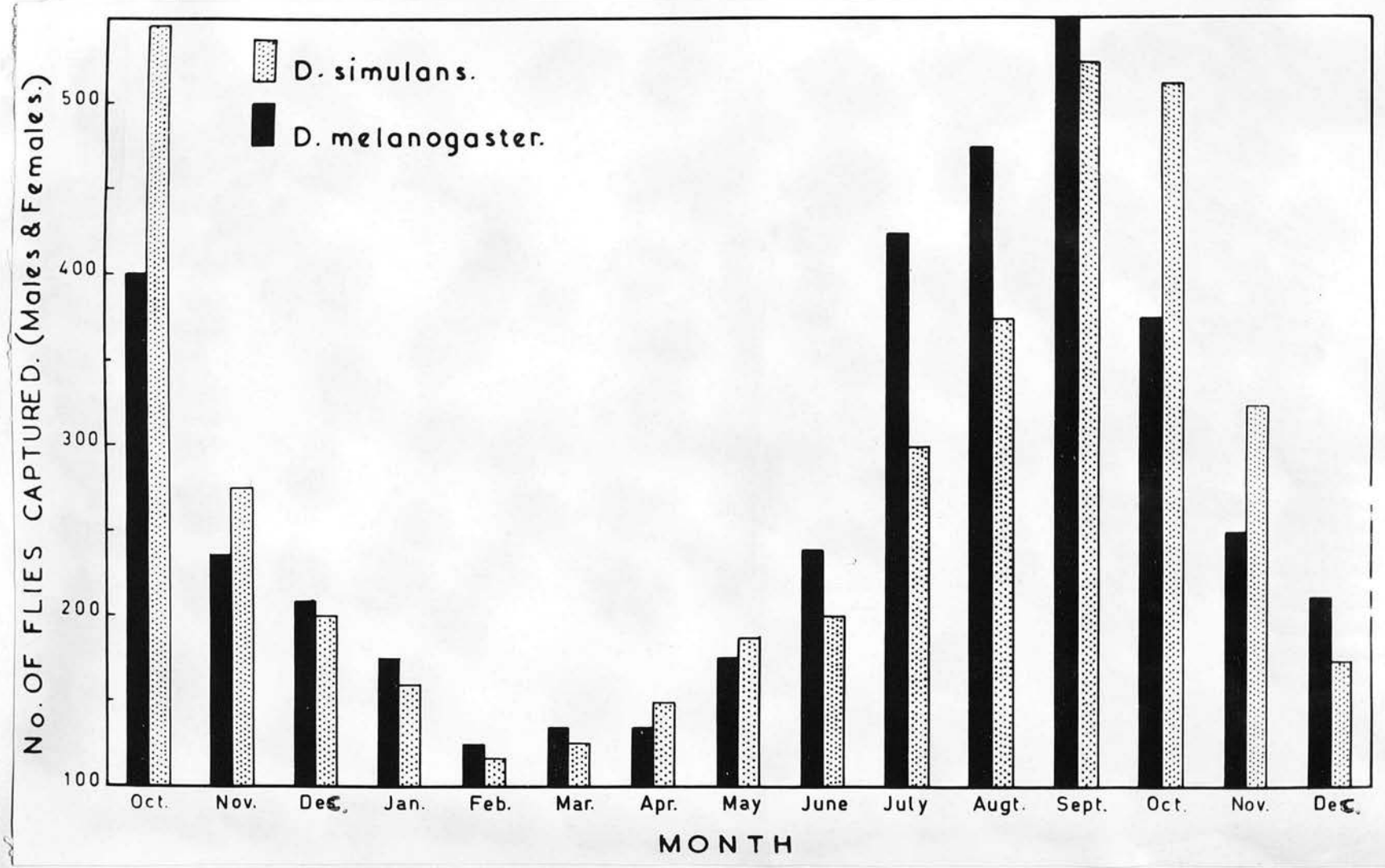

Figure 2. Total number of flies captured per month (both sexes).

Table 1. Percentage of males to the total number (per month) of flies captured.

Months and years	D. melanogaster		D. simulans	
	Total No. of flies	Males%	Total No. of flies	Males%
October,1961	403	47.21	552	45.98
November	237	46.97	276	46.25
December	214	46.95	202	47.76
January,1962	175	48.81	163	48.01
February	125	47.61	116	45.89
March	134	46.56	127	46.41
April	139	48.83	151	47.62
May	175	39.81°	182	38.52°
June	237	38.22°	203	34.29°
July	425	35.21°°	328	30.25°°
August	478	30.22°°	374	29.07°°
September	551	45.83	476	47.62
October	375	48.02	510	46.77
November	250	47.17	325	48.35
December	210	46.39	175	47.09

° Significant at $P < 0.05$

°° Significant at $P < 0.01$

b. Wing length

Figure 3 shows the absolute wing length in each month in different populations. The results indicate that flies from the optimal conditions have the largest wings, while those from the severe conditions have the shortest; both populations show constant wing length throughout the period of study. Test of significance between different laboratory populations indicate significant differences ($P < 0.05$) in most of the months studied. The genetic make up of the "optimal" and "severe" populations may be responsible for such significances since the progeny were raised under identical environmental conditions.

Flies from natural populations show values intermediate (but not significantly so) between optimal and severe laboratory populations, apart from summer months when wing length declines significantly, ($P < 0.05$) as compared with the measurements of wing length of the same populations at other seasons of the year. Similar results were obtained by Stalker and Carson (1949) on Drosophila robusta; they reported that flies captured during the months of August and September showed the smallest wing lengths, with high negative correlation with temperature. Stalker and Carson (1948) also found significant decrease in wing length with decreasing altitude. Tantawy and Mallah (1961) showed significant differences in

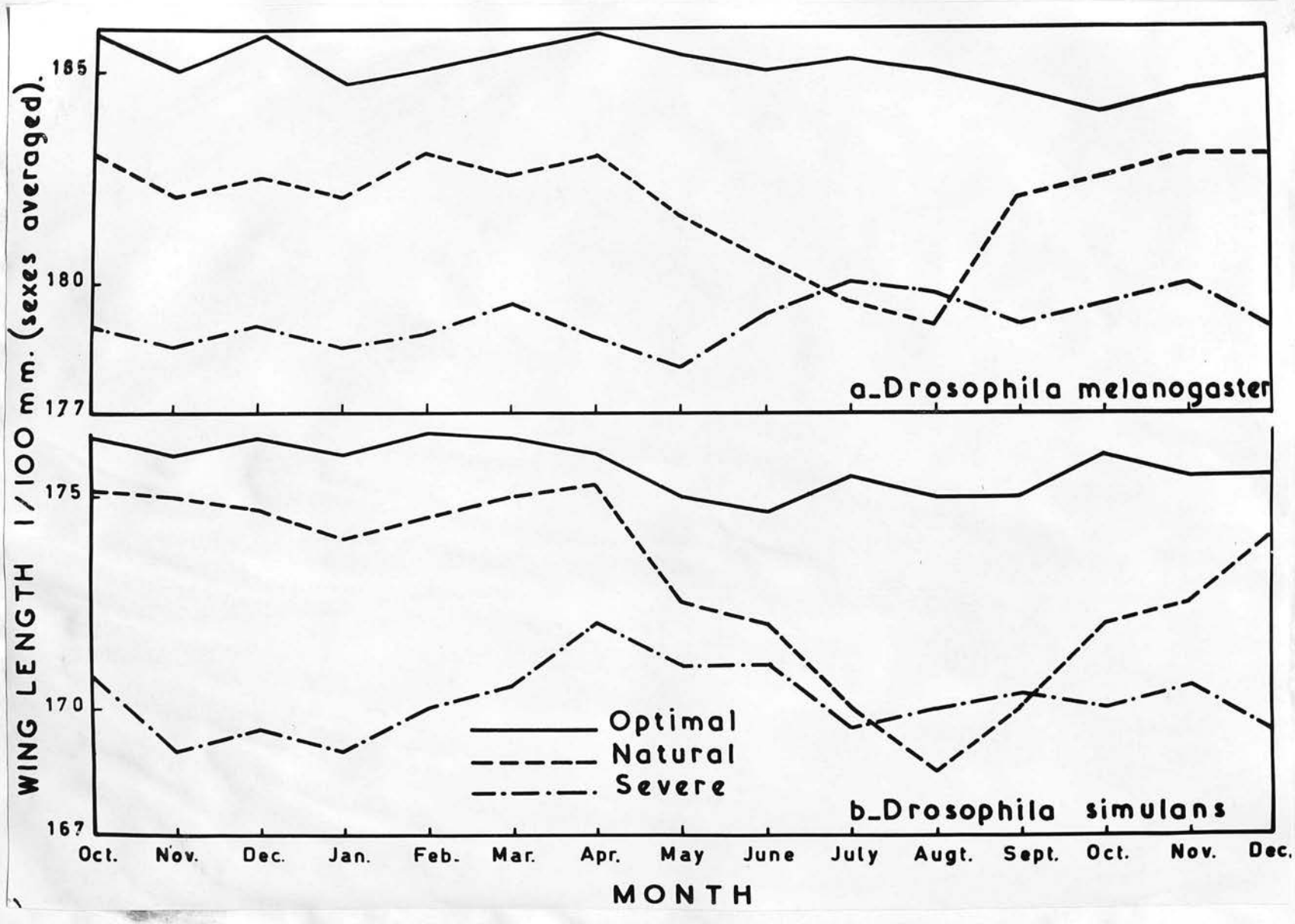

Figure 3. Average wing length (sexes averaged) in each month in various populations (units of measurements are of 1/100 mm).

wing length of Drosophila melanogaster and D. simulans from northern and southern geographical regions. Flies from high altitudes or northern regions are greater in wing length, thus agreeing with the findings of the present study that low temperature increases wing length.

Estimation of the total phenotypic variance (σ^2) of the logarithms of measurements for wing length (table 2) shows insignificant differences within and among various populations. Natural populations of both species of Drosophila show higher variances (but not significantly so) as compared with those of the laboratory ones, apart from those of summer months (July - September, inclusive) for Drosophila melanogaster which shows significantly higher variances ($P < 0.01$) than other populations in the same months.

c. Percentage of emergence

Percentage of emergence was calculated as percentage of adult flies hatched from a given number of eggs. The results for all the populations are presented in figure 4. The results indicate significant differences between both species; Drosophila melanogaster shows higher emergence. Both optimal and severe laboratory populations show almost a constant percentages of emergence (with insignificant differences between them) throughout the period of studies.

Table 2. Variance (σ^2) of logarithms of measurements for wing length in different populations (sexes averaged) in each month. n = 400

Months	D. melanogaster			D. simulans		
	Laboratory		Natural	Laboratory		Natural
	Optimal	Severe		Optimal	Severe	
October (1961)	0.000108	0.000113	0.000118	0.000137	0.000145	0.000189
November	0.000097	0.000114	0.000189	0.000156	0.000161	0.000175
December	0.000113	0.000124	0.000130	0.000187	0.000203	0.000217
January (1962)	0.000120	0.000141	0.000184	0.000209	0.000218	0.000238
February	0.000089	0.000107	0.000115	0.000134	0.000193	0.000251
March	0.000103	0.000142	0.000163	0.000213	0.000224	0.000231
April	0.000112	0.000124	0.000175	0.000228	0.000295	0.000296
May	0.000097	0.000135	0.000178	0.000207	0.000214	0.000219
June	0.000112	0.000130	0.000175	0.000219	0.000245	0.000284
July	0.000105	0.000141	0.000286°	0.000274	0.000281	0.000295
August	0.000123	0.000137	0.000298°	0.000281	0.000291	0.000301
September	0.000110	0.000145	0.000298°	0.000272	0.000281	0.000291
October	0.000113	0.000152	0.000179	0.000271	0.000322	0.000302
November	0.000110	0.000149	0.000185	0.000283	0.000291	0.000297
December	0.000117	0.000162	0.000173	0.000294	0.000305	0.000302

° See text for test of significance

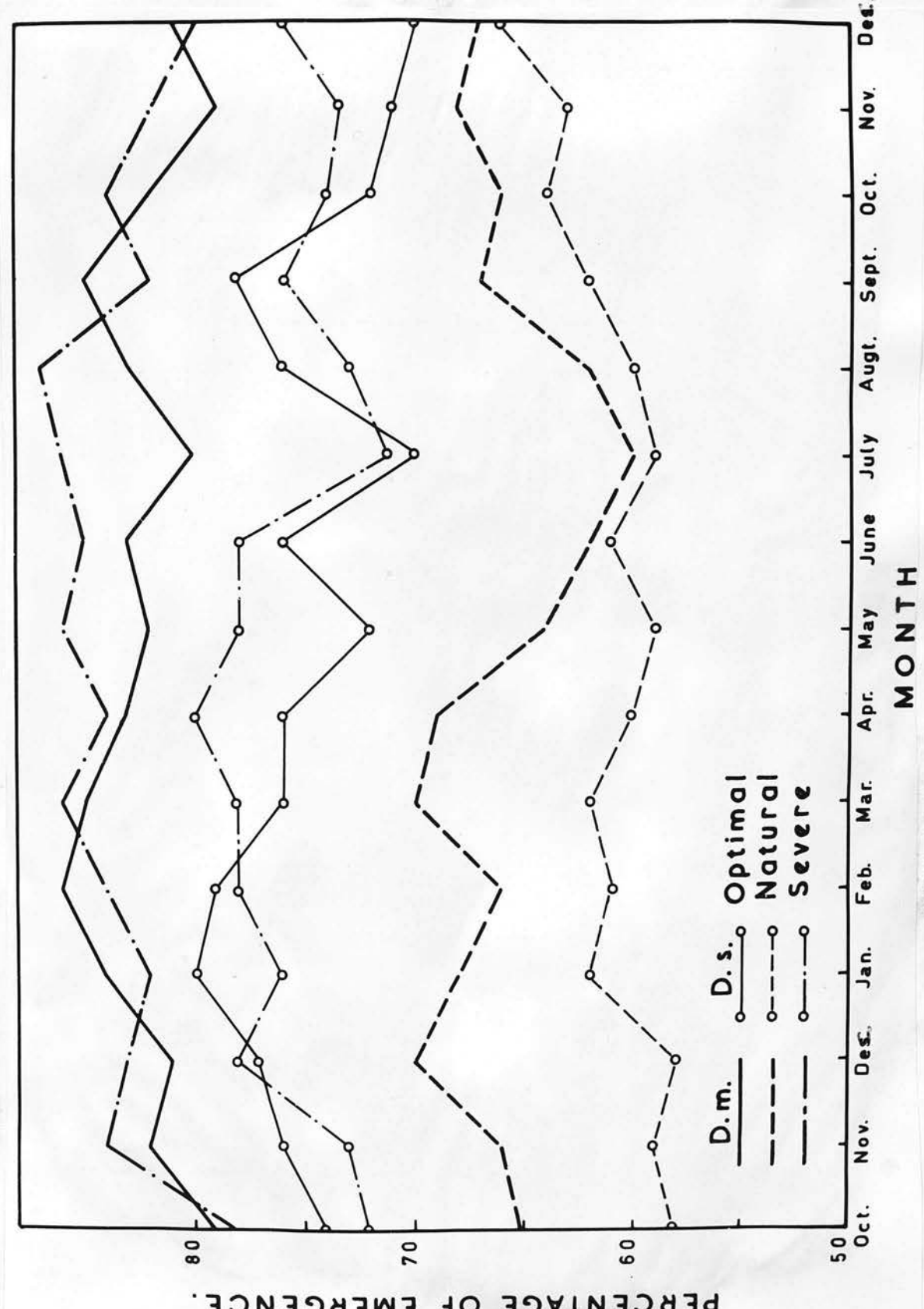

Figure 4. Percentage of emergence in each month in different populations.

Natural populations of Drosophila show percentage of emergence not significantly different from those of the laboratory populations; populations of Drosophila melanogaster give values higher than those of D. simulans. The two species behaved differently; D. melanogaster shows a decrease insignificant during summer months while D. simulans shows a steady rise to the end of the period.

2. Genetical differences

a. Heritability estimates

Heritability of wing length was calculated for each month of the period studied by progeny tests carried out for each population. The method of half-sib analysis was used and the results are presented in table 3 as weighted means per season; each mean was based on monthly estimates within season. The data indicate that, in general, D. melanogaster possesses higher additive genetic variance for wing length than D. simulans. These results agree with those reported by Tantawy et al (1964) working on the same two species. Comparing the genetic variance between different populations, it is clear that populations of both species maintained under optimal conditions show lower but constant values throughout the period of studies.

Populations raised under severe conditions and the progeny tests were carried out also under severe ones show the highest

Table 3. Weighted means for the percentage of the heritability estimates at different seasons (based on monthly values per season) for wing length, with their respective standard errors.

Seasons and years	Laboratory populations		Natural populations
	Optimal	Severe	
a. Drosophila melanogaster			
Autumn,1961	33.75 ± 3.14	49.81 ± 4.74	39.92 ± 2.94
Winter,1962	34.49 ± 2.58	53.61 ± 3.39	42.18 ± 4.32
Spring,1962	32.64 ± 3.10	49.53 ± 4.04	40.29 ± 3.75
Summer,1962	34.37 ± 4.09	52.10 ± 4.18	29.77 ± 3.25°
Autumn,1962	35.62 ± 3.85	48.92 ± 3.79	37.66 ± 3.17
Winter,1963	34.27 ± 3.06	50.34 ± 3.82	41.32 ± 3.79
Spring,1963	31.95 ± 3.15	48.43 ± 3.87	40.01 ± 3.65
Summer,1963	35.97 ± 2.97	47.53 ± 3.76	23.75 ± 3.42°
Autumn,1963	31.42 ± 3.14	49.95 ± 4.14	49.48 ± 4.06
b. Drosophila simulans			
Autumn,1961	31.36 ± 3.18	49.76 ± 4.11	29.36 ± 3.27
Winter,1962	30.36 ± 4.07	52.84 ± 5.33	36.46 ± 4.18
Spring,1962	28.14 ± 3.46	50.49 ± 4.82	35.98 ± 3.18
Summer,1962	28.94 ± 3.27	52.18 ± 5.07	39.43 ± 3.87
Autumn,1962	29.96 ± 3.29	46.18 ± 3.97	33.96 ± 4.18
Winter,1963	32.24 ± 4.15	51.75 ± 4.18	34.76 ± 3.74
Spring,1963	29.01 ± 3.75	48.97 ± 4.97	34.85 ± 3.37
Summer,1963	35.34 ± 3.54	47.18 ± 4.18	40.98 ± 2.89
Autumn,1963	36.86 ± 3.52	50.85 ± 3.75	35.87 ± 3.87

Table 3. Cont.

c. "Severe" laboratory populations: Progeny tests were carried out at optimal conditions.

	D. melanogaster	D. simulans
Autumn, 1962	31.23 ± 3.15	28.65 ± 3.16
Winter, 1962	29.74 ± 2.74	28.25 ± 3.47

° See text for test of significance

heritability estimates. On the other hand, when the progeny tests from the severe populations were carried out under optimal conditions (table 3c) genetic variance has the smallest values. Thus, the results indicate that populations raised under severe conditions show a higher level of genetic variability; this might result from a greater variety of niches in the fluctuating environment. Beardmore (1961) reported that Drosophila populations of common ancestory raised under various environmental conditions differed in their additive genetic variance; fluctuating environment gave higher heritability estimates.

The most interesting features of the present study are those obtained from the natural populations. The two species of Drosophila behaved differently; D. simulans shows a rise though insignificantly so, in the heritability estimates from 29.36 ± 3.27 percent in Autumn 1961 to 36.46 ± 4.18 in winter 1962 and then stays more or less constant. Populations of D. melanogaster show constant values throughout the period apart from summer seasons of 1962 and 1963, when the heritability values decline significantly ($P < 0.05$) as compared with the results obtained in the other seasons.

b. Phenotypic, genetic and environmental correlations between wing and thorax lengths

The total phenotypic correlation between wing (W) length and thorax (T) length in populations of Drosophila, i.e.

$r_{P_W P_T}$, can be devided into its genetic and environmental components as follows:

$$r_{P_W P_T} = h_W h_T r_{G_W G_T} + e_W e_T r_{E_W E_T}$$

Where,

h_W and h_T = square root of the heritability estimate for wing and thorax lengths, respectively.

$r_{G_W G_T}$ = genetic correlation between wing and thorax lengths.

e_W and e_T = $\sqrt{1 - h_W^2}$ and $\sqrt{1 - h_T^2}$, respectively.

From the previous equation the environmental correlation ($r_{E_W E_T}$) between wing and thorax length can be worked out since $r_{G_W G_T}$ can be estimated from the half-sib covariances. Monthly correlations between the two dimentions in both species of Drosophila are presented in figure 5. The results indicate that various correlations in optimal and severe populations remain almost constant from month to month; both species behaved similarly. Significant differences ($P < 0.01$) were observed in the total phenotypic and environmental correlations between the different laboratory populations; optimal populations show higher values. On the other hand, genetic correlation ($r_{G_W G_T}$) do not show such significant differences.

Correlation coefficients in natural populations are different. The values remain almost constant in D. melanogaster

throughout the experimental period apart from those of the summer months, when they decline significantly ($P < 0.05$) as compared with other values. The total phenotypic correlation in D. simulans remains almost constant among months, genetic correlation declines significantly in summer months, while environmental correlation shows its only significant decline in September and October of both years.

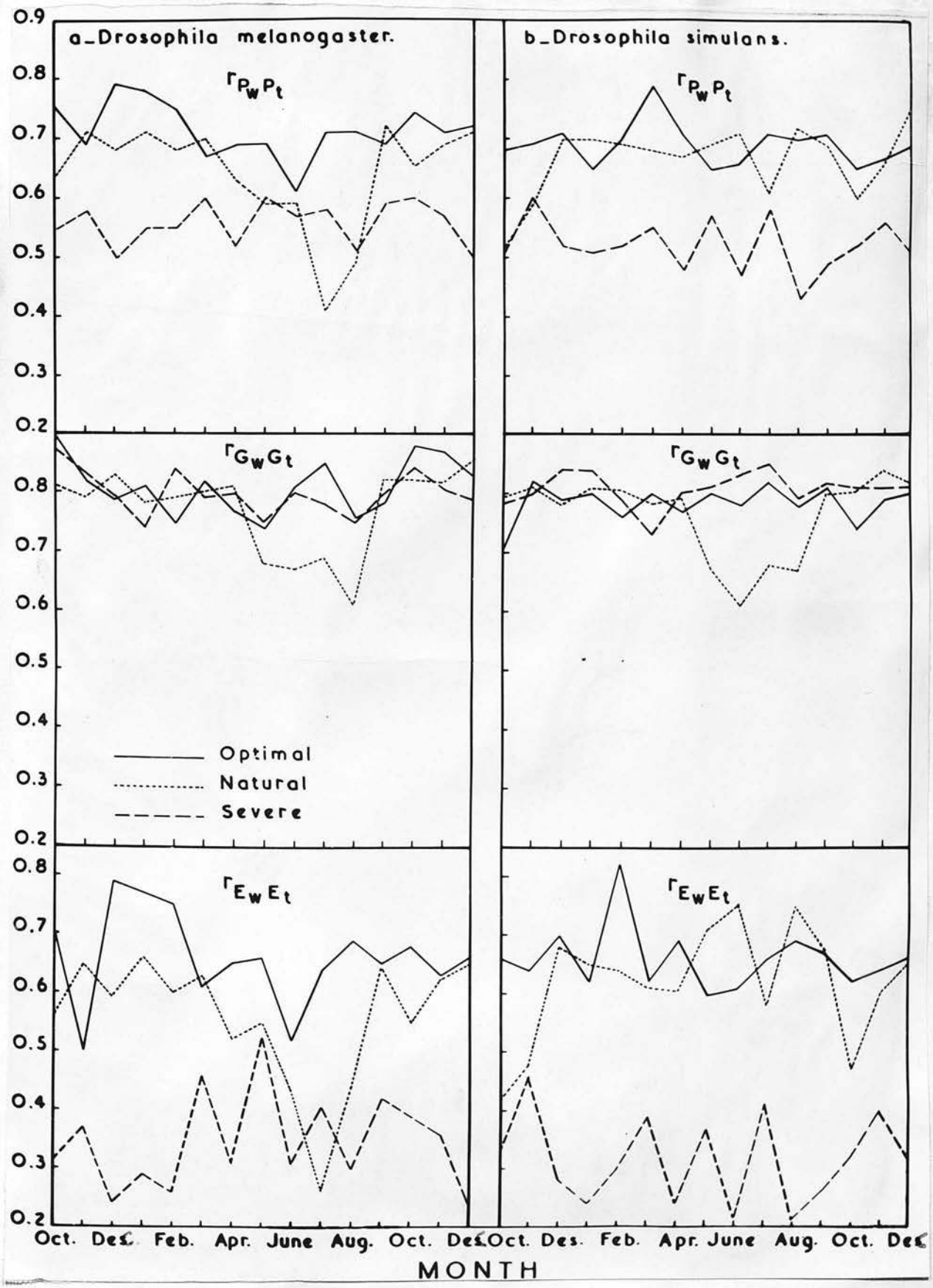

Figure 5. Total phenotypic, genetic and environmental correlations between wing and thorax length in each month

Conclusions

Recent results indicate that different wild species of Drosophila react differently in their adaptive adjustments to seasonal changes. Dobzhansky (1943) studying Drosophila pseudoobscura and Dubinin (1945) working on Drosophila funebris were the first to report genetic differences related to seasonal variation (but see Timofeeff-Ressovsky, 1940 for similar report on another organism). They pointed out that carriers of different gene-arrangements may be favoured or discriminating against by environmental agencies. Stalker and Carson (1949) attributed seasonal and altitudinal morphological differences between strains of Drosophila robusta to the adjustment of the various inversion frequencies.

The seasonal morphological differences observed in the present study on natural populations of Drosophila melanogaster and D. simulans indicate a significant decline in wing length during summer months, i.e. with highest temperature and humidity. Such a decrease in wing length is due mainly to temperature effects (Tantawy and Mallah 1961) as food resources are abundant throughout summer. Thus winter and summer seasons tend to resemble latitudinal changes in their effects on Drosophila size. These results are in agreement with those reported by Stalker and Carson (1949).

Genetic variance in Drosophila melanogaster at various seasons of the year indicates that environmental conditions

in summer cause a significant decrease in the heritability estimates for wing length; the situation in D. simulans is different, genetic variance remains almost constant. These results indicate that the species react differently to environmental conditions. The two species contrast sharply; Drosophila melanogaster is very frequently chromosomally polymorphic (Patterson and Stone 1952) while D. simulans has not been observed to deviate from a strict chromosomal monomorphism. Previous studies of both species (Mourad and Mallah 1960) captured in the same region as for the present studies support the findings of Patterson and Stone. Dobzhansky (1947) stated that the inversion mechanism may facilitate adaptation to different ecological niches in the same geographical environment. There is abundant evidence from the field and laboratory experiments in Drosophila that the chromosomal polymorphs are means for adaptation to environmental changes. Cyclic seasonal changes in the relative frequencies of karyotypes of Drosophila pseudoobscura have been reported by Dobzhansky (1961). Therefore, one may conclude that differences in the genetic make-up of the two species may be responsible for the different behaviour in the genetic component of variance in wing length.

During winter, temperature and humidity are relatively low and food is scarce, as compared with summer. It seems

reasonable that if environmental conditions are changed, the fitness of some karyotypes may either improve or deteriorate in relation to that of other karyotypes. Natural selection will enhance the frequencies of the more fit and depress those of less fit karyotypes. Dobzhansky (1962) stated that " A living species always faces a variety of environments; adaptation to multiplicity of environments can be achieved in two ways. First, genotypes are favored by natural selection which confer upon their carriers the property of homeostasis, physiological or developmental buffering, in the range of the environments which the species normally meets. Secondly, another form of natural selection (diversifying or disruptive selection) favors a genotypic variety or polymorphism, the different genotypes making their carriers relatively fitter in different environments".

Considering variability, in the present study, between populations within species and between months within populations, it is generally clear that greater fitness (figure 3) is associated with lower variability (table 2). Total phenotypic variation for a given trait may be caused by genetic, environmental agencies and interaction of both. Robertson and Reeve (1952) reported that adaptation to environment in Drosophila melanogaster depends on heterozygous

genotypes, where heterozygosity causes more uniform phenotypes than homozygosity. Similar results were obtained by Tantawy (1961) for Drosophila pseudoobscura.

Summary

The present experiments were designed to study morphological and genetical differences in various populations of Drosophila melanogaster and D. simulans through the period of October, 1961 to December, 1962. Populations used are one of each species in nature and two in the laboratory. One of the latter for each species was reared under optimal conditions and the other under severe one. The following results were obtained:

1. Collections of flies from the natural populations indicate that both species are more abundant in summer than in winter. Drosophila melanogaster dominates D. simulans throughout the period of the study apart from September to December of both years when the latter species was more abundant.

2. Sex-ratio in natural populations of both species of Drosophila is almost constant; females are in excess though insignificantly so except in summer months when males are in significantly less numerous than females. Sex-ratio in the laboratory populations remain almost constant throughout the period, females being slightly in excess. Wing length remains

almost stable; the "severe" population has shorter wing length than that reared under optimal conditions. Natural populations show a significant decrease in wing length in summer.

3. Percentage of emergence of adults (from known number of eggs) behaves differently in natural populations of Drosophila melanogaster and D. simulans, with D. melanogaster generally significantly higher. In the summer D. melanogaster shows an insignificant decline in percentage of emergence and D. simulans showed a steady rise from October, 1961 to December, 1962.

Laboratory populations do not change in this respect with season and there are no differences between different populations.

4. Heritability estimates for wing length in natural populations are greater for Drosophila melanogaster than D. simulans. The results indicate that the heritability of wing length remaines fairly constant in D. simulans during all months of the year while D. melanogaster shows a significant decline in the heritability estimates during summer. On the other hand, laboratory populations show constant values with significant differences between different conditions.

5. Total phenotypic correlation between wing and thorax length, genetic correlations, and environmental ones were

calculated and discussed.

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The author wishes to express his gratitude and indebtness to Professor R. C. Lewontin for his suggestions in the experimental work during his short visit to Alexandria in summer 1962. His advice and criticism during the preparation of the manuscript are very much appreciated.

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Editorial Office, GENETICS
Dept. Biological Sciences
Stanford University
Stanford, California
September 8, 1964

Dr. A. O. Tantawy
Faculty of Agriculture
University of Alexandria
Alexandria, U. A. R.

Dear Dr. Tantawy:

The paper, "Studies on natural populations of Drosophila. IV. Genetic variances of and correlations between four characters in D. melanogaster and D. simulans," has been accepted and will be scheduled for the December issue of GENETICS. The authors are A. O. Tantawy and F. A. Rakha.

Sincerely,

David D. Perkins

David D. Perkins
Editor

DDP/JT

STUDIES ON NATURAL POPULATIONS OF DROSOPHILA.
IV. GENETIC VARIANCES OF AND CORRELATIONS BETWEEN FOUR CHARACTERS IN DROSOPHILA MELANOGASTER AND D. SIMULANS.

A. O. TANTAWY and F. A. RAKHA
Faculty of Agriculture, University of Alexandria, Alexandria, Egypt, U. A. R.

Resemblance between relatives with respect to a given quantitative character is a basic genetic phenomenon; the degree of resemblance determines the amount of additive genetic variance. The causes for such resemblance are related not only to genetics but also to environment. Therefore, the phenotypic value for a given individual is the sum of genetic and environmental effects (REEVE and ROBERTSON 1953).

Most characters in Drosophila are highly responsive to environmental changes (TANTAWY and MALLAH 1961) and only a proportion of the total phenotypic variance is actually accounted for by gene action. In selection programs (e.g., TANTAWY, MALLAH and TEWFIK 1964) it is essential, in some

experiments, to devide the total variation of a given trait into its various components, particularly that component due to the additive gene effects. Correlation coefficients between various characters are needed; the genetic correlation is important because the response to selection for the primary character may influence the secondary characters (REEVE and ROBERTSON 1953; CLAYTON, KNIGHT, MORRIS and ROBERTSON 1957).

The present experiments were designed to study the genetical and environmental effects on the total phenotypic value for a given character in populations of two Drosophila species. Heritability estimates were made for each of the characters wing length, thorax length, longevity of adult flies and lifetime egg production, and correlation coefficients were determined between each pair.

TECHNICAL PROCEDURE

The initial foundation population: Populations used in the present experiments are similar to those used by TANTAWY and MALLAH (1961) which were captured at the University of Alexandria Farm. In each species eggs (not more than 70 per vial) from the mass-mating population were cultured in well yeasted food vials in ten replicates. After emergence, virgin females were separated from males. Twenty pairs, ten on each day, from each replicate (given a total of 200 pairs) were

measured for wing and thorax length. The measured flies were also used for estimating the lifetime egg production and the longevity of both sexes. Measurements of wing and thorax lengths, lifetime egg production and longevity were carried out as described by TANTAWY (1961a).

Progeny tests: Eggs from both species were cultured as before in 20 food vials. After emergence virgin females were obtained and 20 pairs of flies from each vial, ten on each day, were measured for wing and thorax lengths. Random pair-matings were carried out within the measured flies of each vial; lifetime egg production and longevity were also estimated. Eggs from the 400 pair matings were cultured in food vials, and after emergence of the F_1 progeny virgin females were also obtained. Five males and five females from the progeny of each pair mating were used for measuring wing and thorax lengths, as well as lifetime egg production and longevity. Heritability of each character was estimated by doubling the phenotypic correlation between mothers and daughters. Since the statistical analyses indicate no significant differences between replicates the results were therefore combined and presented as weighted means.

All the experimental work were carried out under optimal constant temperature of $25 \pm 0.05^{\circ}$C.

RESULTS

Comparisons between Drosophila melanogaster and Drosophila simulans: Table 1 shows the absolute means for the four different characters studied. The results indicate clearly that the species are different; the former displays greater measurements for each trait than the latter, and females of Drosophila melanogaster lay significantly ($P < 0.01$) more eggs. Moreover, TANTAWY and MALLAH (1961) reported that eggs of D. melanogaster are the more viable. In both species females are significantly longer ($P < 0.01$) in wing length than males, and females of both species live no significant longer than males.

Total phenotypic correlations: Table 2 presents the various correlation coefficients between the characters studied. There are clearly significant positive correlations between the different characters which raises the question as to the origin of such an association and whether it is due to environment, to heredity or to both?. SANG (1950) has noted that the smaller flies which result from crowded conditions during growth lay fewer eggs. ROBERTSON (1957b) reported similar positive correlations between body size and egg production in D. melanogaster. TANTAWY and VETUKHIV (1960) and TANTAWY (1961b) showed positive correlations among the

same four characters used in the present study, but in D. pseudoobscura; a given reduction in D. pseudoobscura leads to a proportional reduction in egg production and longevity as well.

Table 1. Means (1/100 mm) for wing length, thorax length; longevity (days) and lifetime egg production (average per female) with their respective coefficients of variation, C.V. n = 200

Characters	D. melanogaster				D. simulans			
	Males		Females		Males		Females	
	Means	C.V.	Means	C.V.	Means	C.V.	Means	C.V.
Wing L. (W)	175.32	2.95	204.17	3.20	173.69	3.89	200.83	3.62
Thorax L. (T)	89.25	3.95	103.25	3.72	85.85	4.27	100.11	4.49
Longevity (L)	14.06	29.44	14.80	31.01	8.95	34.52	12.59	32.84
Lifetime egg prod. (G)	-----	----	389.50	60.12	-----	----	191.75	80.23

Table 2. Observed total phenotypic correlations between the four different characters°. d.f. = 380

Correlations between	D. melanogaster	D. simulans
W - T	0.5775 ± 0.116	0.5840 ± 0.098
W - G	0.2440 ± 0.137	0.2189 ± 0.118
W - L	0.2197 ± 0.138	0.2143 ± 0.124
T - G	0.5055 ± 0.112	0.2508 ± 0.117
T - L	0.3315 ± 0.133	0.1190 ± 0.112
L - G	0.7568 ± 0.137	0.4035 ± 0.110

° For symbols see Table 1

Heritability estimates: It seems to be very important to give all the observed parent (mothers) - offspring (daughters) correlations for both species (Table 3) which includes not only the correlations with respect to the same characters but also the cross correlations, e.g. parent's wing vs offspring's thorax. The results indicate positive correlations between different characters. The parent offspring correlation ($r_{P_X O_X}$) was used in estimating the heritability ($h^2 = 2r_{P_X O_X}$) of each character and $e^2 = 1 - h^2$, the results are presented in Table 4, where "h" and "e" have their usual meanings and usefulness. The results indicate clearly that metric characters are more heritable than fitness ones. The value of h^2 expresses the proportion of the total variance that is attributable to the average effects of genes; this is what determines the degree of resemblance between relatives. The total variation for a given character includes additive, non-additive and environmental causes; non-additive causes play a great role in the total variation of fitness characters than the mertic ones. Similar results were reported by ROBERTSON (1957b).

Knowledge of the degree of the correlation between phenotypic and breeding values, i.e. h, for a given trait is important in the prediction of the response to selection.

Table 3. Parent-offspring correlations° (e.g., wing vs wing) and the cross correlations (e.g., wing vs thorax), with their respective standard errors

Parents	Offspring W	Offspring T	Offspring L	Offspring G
a. Drosophila melanogaster				
W	0.1231±0.032	0.0819±0.021	0.0150±0.025	0.0005±0.039
T	0.0957±0.025	0.1017±0.020	0.0104±0.037	0.0014±0.048
L	0.0750±0.049	0.0889±0.034	0.0564±0.043	0.0058±0.033
G	0.0019±0.054	0.0014±0.042	0.0004±0.038	0.0128±0.026
b. Drosophila simulans				
W	0.1090±0.031	0.1780±0.022	0.0303±0.024	0.0004±0.038
T	0.0436±0.034	0.1165±0.025	0.0221±0.041	0.0010±0.051
L	0.0708±0.045	0.1228±0.036	0.0730±0.045	0.0030±0.038
G	0.0026±0.049	0.0015±0.039	0.0014±0.039	0.0556±0.037

° For symbols see Table 1

Table 4. Heritability ($h^2 = 2r_{P_X O_X}$), $e_X^2 = 1 - h_X^2$ for each character as well as "h" and "e". Number of matings=400

Characters°	h^2	e^2	h	e
a. Drosophila melanogaster				
W	0.2462	0.7538	0.4962	0.8682
T	0.2034	0.7966	0.4510	0.8926
L	0.1129	0.8871	0.3360	0.9419
G	0.0257	0.9743	0.1603	0.8971
b. Drosophila simulans				
W	0.2180	0.7820	0.4669	0.8843
T	0.2330	0.7670	0.4827	0.8758
L	0.1460	0.8540	0.3821	0.9241
G	0.1112	0.8888	0.3355	0.9428

° For symbols see Table 1

The results indicate that the breeding values for metric characters are higher than those of fitness ones, while the "e" values are reversed in favor of the latter characters. These results agree with those reported by ROBERTSON (1957b) in showing the gradation of the heritability estimates for metric characters and finess ones in Drosophila melanogaster.

Genetic and environmental correlations: Estimates of the genetic (r_G) and environmental (r_E) components of the phenotypic correlations, e.g. between the two characters X and Y, could be given from the following equations : where P and O denote parents and offspring, respectively.

$$r_{G_X G_Y} = 2\sqrt{r_{P_X O_Y} r_{P_Y O_X}} \; / \; h_X h_Y$$

$$r_{E_X E_Y} = \left[r_{O_X O_Y} - h_X h_Y r_{G_X G_Y} \right] / \; e_X e_Y$$

The quantities $r_{G_X G_Y}\, h_X h_Y$ and $r_{E_X E_Y}\, e_X e_Y$ should add up exactly to r_{XY} of Table 2.

The results obtained from the present experiments for the genetic and environmental correlations between different characters in both species of Drosophila are presented in Table 5. The results for the genetic correlation (r_G) between wing-thorax lengths, wing length-longevity and thorax-longevity are high, in both species, which indicate that flies of longer wing length have longer thorax length and live longer time than small flies. These results agree with the findings of TANTAWY and VETUKIV (1960) in Drosophila pseudoobscura. Other genetic correlations, particularly those with egg production, are very low; indicating that a change made by selection for wing

Table 5. Genetic (r_G) and environmental (r_E) correlations between different characters°. d.f. = 380

Items	Correlation between					
	W-T	W-G	W-L	T-G	T-L	L-G
a. *Drosophila melanogaster*						
(1) $2\sqrt{r_{P_XO_Y} r_{P_YO_X}}$	0.1771	0.0020	0.0671	0.0028	0.0608	0.0030
(2) $h_X h_Y$	0.2238	0.0795	0.1667	0.0723	0.1515	0.0539
(1)/(2)=$r_{G_XG_Y}=r_G$	0.7913	0.0252	0.4025	0.0387	0.4013	0.0557
(3) $r_{O_XO_Y}$	0·5775	0.2440	0.2197	0.5055	0.3315	0.7588
(4) (3) - (1)	0.4004	0.2420	0.1526	0.5027	0.2707	0.7538
(5) $e_X e_Y$	0.7749	0.8570	0.8178	0.8810	0.8406	0.9297
(4)/(5)=$r_{E_XE_Y}=r_E$	0.5167	0.2824	0.1866	0.2706	0.3220	0.8108
b. *Drosophila simulans*						
(1) $2\sqrt{r_{P_XO_Y} r_{P_YO_X}}$	0.1762	0.0020	0.0926	0.0025	0.1042	0.0041
(2) $h_X h_Y$	0.2254	0.1557	0.1784	0.1610	0.1844	0.1274
(1)/(2)=$r_{G_XG_Y}=r_G$	0.7817	0.0128	0.5191	0.0155	0.5651	0.0322
(3) $r_{O_XO_Y}$	0.5840	0.2189	0.2143	0.2508	0.1190	0.4035
(4) (3) - (1)	0.4078	0.2169	0.1217	0.2483	0.0148	0.3994
(5) $e_X e_Y$	0.7745	0.8337	0.8172	0.8257	0.8093	0.8712
(4)/(5)=$r_{E_XE_Y}=r_E$	0.5265	0.2602	0.1489	0.3007	0.0183	0.4584

° For symbols see Table 1

length in Drosophila is not accompanied with similar change in lifetime egg production. REEVE (1954) reported, in spite of the value of 0.27 as the genetic correlation between body size and egg production in Drosophila melanogaster, that a change in the former character made by selection did not lead to a parallel change in the latter one. ROBERTSON(1957b) reported that, in only one comparison after five generations of selection, there was clear evidence of correlated change in egg production; in others, the differences in the output between large, small and unselected strains are negligible.

Environmental correlation (r_E) between different traits, which is due to the correlation of environmental deviations together with non-addtive genetic ones, shows how the genetic and environmental causes of correlation combine together to give the total phenotypic correlations. The results (Table 5) indicate that if both characters possess low heritability estimates (e.g., longevity and egg production) then the phenotypic correlation between them is determined chiefly by environmental correlation, and on the other hand if they display high additive genetic variance (e.g., wing and thorax length) then the genetic correlation is more important. The results obtained for wing and thorax lengths confirm those given by REEVE and ROBERTSON (1953) who reported the values

of 0.75 and 0.50 as genetic and environmental correlations, respectively. REEVE and ROBERTSON (1954) stated that " The genetic and environmental variations affecting a quantitative character should at least partly mimic each other's effects, since they must often influence the same chemical processes. Thus, both genetic and environmental factors affecting wing and thorax length in Drosophila cause partly correlated and partly uncorrelated variations, so that the genetic and environmental correlations are typically of the same order". The present results agree, in general, with those reported by the previous authors.

Conclusions

For a detailed study of the genetic variance in wild populations of Drosophila, it is essential to investigate and compare the properties of the genetic variation in many different characters. Various authors attacked such a problem in Drosophila melanogaster, e.g. ROBERTSON and REEVE (1952); REEVE and ROBERTSON (1953); TANTAWY (1964) and TANTAWY et al (1964) working on body size, CLAYTON et al (1957) on bristle number, ROBERTSON (1957a) on ovary size and ROBERTSON (1957b) on egg production. The present investigation adds more information on the inheritance of quantitative characters in both Drosophila melanogaster and D. simulans and the relationship between some of the different characters

namely wing length, thorax length, longevity and lifetime egg production.

The results as presented in Tables 1 and 4 indicate clearly that characters with lower heritability estimates show greater phenotypic variance. Similar results were reported by ROBERTSON (1957b) on D. melanogaster and TANTAWY (1961b) on D. pseudoobscura. It is interesting, however, to note that fitness characters of lower heritability estimates experienced the greatest reduction during inbreeding than metric ones, TANTAWY (1959).

The higher heritability estimates for wing and thorax length indicate that selection for longer or shorter dimensions is more effective than that for egg production or longevity. These results agree with those reported by different investigators working on such a problem, for review and references see TANTAWY et al (1964). The genetic correlation can be utilized more accurately as basis for selection for a given character than the phenotypic one if both are estimated with equal accuracy. For instance, selection for wing length would be accompanied by a similar change in the same direction for thorax length or vice versa (ROBERTSON and REEVE 1952; REEVE 1954; TANTAWY 1959 and TANTAWY et al 1964), to a lesser degree for longevity, but not for egg production (ROBERTSON 1957b). From the various correlation coefficients,

one may conclude that egg production is correlated with body size and with longevity through non-additive gene effects; gene-environment interaction may play a great role in such association. This is likely to be important in view of the sensitivity of growth to nutritional variation (ROBERTSON 1963). If most individuals never attain their maximum potential size, large individuals will be favoured by virtue of their greater output and might expect a clear cut correlation between body size and egg production and probably also growth rate.

Few experiments have been performed to check the adequacy of the response to selection for a primary character on correlated ones. For instance, REEVE (1954); CLAYTON et al (1957) and ROBERTSON (1957a,b) all reported that the observed response to selection for a given metric character in Drosophila melanogaster fits well with the theoretical expectation. Therefore, the next paper will deal with long term two-way selection for wing length and its effects on the other three correlated characters.

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SUMMARY

The present experiments were carried out to investigate the various correlation coefficients between four different characters, i.e. wing length, thorax length, lifetime egg production and longevity of adult flies.

The total phenotypic ($r_{O_X O_Y}$) and the cross correlations ($r_{P_X O_Y}$) between each two characters indicate clear positive values. Wing and thorax lengths display higher heritability estimates ($h^2 = 2r_{P_X O_X}$) than egg production or longevity in both species of Drosophila melanogaster and D. simulans.

Genetic correlations involving wing length, thorax length and longevity are high while those including egg production are very low; all the genetic correlations are positive.

Environmental correlations between different characters were calculated and discussed.

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Studies on natural populations of Drosophila. V. Correlated response to selection in Drosophila melanogaster

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Quite a number of experiments have been designed to study the response to selection in Drosophila; most of them deal with the comparison between response to selection for a given metric character with changes in one or more traits. ROBERTSON and REEVE (1952b); REEVE and ROBERTSON (1953, 1954); TANTAWY (1959) and TANTAWY, MALLAH and TEWFIK (1964) working with wing length in Drosophila melanogaster and RASMUSSON (1955); CLAYTON, MORRIS and ALLAN ROBERTSON (1957) and CLAYTON, KNIGHT, MORRIS and ALLAN ROBERTSON (1957) selecting different bristle number in Drosophila melanogaster, reported that selection for the primary character was accompanied by

correlated changes in other characters.

Nevertheless few experiments have been carried out to study how the response to selection for a given metric character involves correlated changes in components of fitness. ROBERTSON (1957b) reported that selection for wing length in Drosophila melanogaster did not lead to correlated changes in egg production but in the all the selected lines egg viability decreased. TANTAWY and VETUKHIV (1960) reported that selection for long or short wing length, for only one generation in Drosophila pseudoobscura, was accompanied by similar changes in thorax length, the longevity of adult flies and also lifetime egg production as well.

The present experiments were undertaken to study the effects of long-term two-way selection for wing length in Drosophila melanogaster on other three character, i.e. thorax length, the longevity of adult flies and egg production. Selection was carried out in plus and minus directions with two different systems of mating,i.e. brother-sister and outbreeding. The selected inbred lines were crossed at a known level of homozygosity to study the percentage of heterosis in all the characters.

TECHNICAL PROCEDURES

Initial foundation population

A population of Drosophila melanogaster, from flies captured early in 1962 at the University of Alexandria Farm, was the basis of the present investigations. Further details of locality, crosses between the captured flies and handling of the initial population, are given by TANTAWY and MALLAH (1961).

The characters studied

Wing and thorax lengths of the live flies were measured by an instrument devised by ROBERTSON and REEVE (1952b). Eggs from pair matings were collected by the methods reported by these authors and the longevity of the adult flies was estimated in the manner described by TANTAWY (1961).

Experimental design

a. Characters of the base population

Heritability of the four different characters studied, i.e. wing length, thorax length, longevity and lifetime egg production were estimated in the initial foundation population before starting the selection experiments. Eggs from the mass mating population were cultured in ten food vials (not more than 70 per vial) for five successive days and after emergence virgin females from each vial were obtained. Twenty

pairs of flies from the progeny of each vial, giving a total of 200 pairs, were measured for wing and thorax length. The measured flies were then mated at random in pairs; lifetime egg production was noted daily from each pair and at the same time the longevity of both sexes was determined. Eggs from each pair mating were cultured in food vials for five successive days and after hatching of the progeny, virgin females were collected. Ten pairs of flies, on two days, from each parental pair were measured for wing and thorax lengths, and then mated (5 pairs per vial) at random. The lifetime egg production and longevity of both sexes were estimated. These data provide relevant information about the four different characters in the base population, including heritability estimates (by doubling the correlation between mothers and daughters) and all the possible genetic correlations between few of the characters.

b. Selection procedures

Two different selection experiments were carried out in succession; the first involved matings between full sibs and the other between unrelated individuals, these will be considered in this order.

1. Full sib matings

This experiment was started from the F_2 generation of the captured females; matings were carried out between full

brothers and sisters for nine successive generations. Four selected lines were maintained, two plus and two minus lines. The selection experiment was carried out in the following way:

Four vials of eggs were maintained from the mass mating population and after emergence virgin females were separated from males. Twenty pairs of flies from each vial were measured for wing and thorax length. Five selected pairs from the progeny of each of the vials No. 1 and 2 were set up and assortative matings were made between the largest male and the largest female to establish the two selected lines (A and B) in the plus direction. Progeny resulting from vials No. 3 and 4 were used to initiate the two lines (C and D) in the minus direction. The procedure was similar to that in the plus direction except that the assortative matings were between the smallest flies. Each plus and minus line was always continued from the largest or smallest pairs, respectively.

Eggs from the selected pairs were counted daily from the 5th. day up to the 10th. and cultured separately in well yeasted vials. At each generation of selection twenty pairs of flies , on two days , were measured for wing and thorax length in each of the selected inbred lines and the selection procedure was repeated for nine generations.

A control population was kept mass mating under similar environmental conditions to those of the inbreds and at each generation 20 pairs of flies on the same two days were measured for wing and thorax length.

Correlated characters

Longevity of adult flies was estimated in the selected lines and the control population at the 1st., 3rd., 6th. and at the 9th. generations of selection by taking samples of 100 pairs from each line. After measuring their wing and thorax lengths, each pair of flies was kept in an oviposition vial. All the flies used in the test were collected within twenty four hours. The surviving adults in each vial were transferred daily to fresh ones and the number of deaths in both sexes were recorded. The daily egg production from each pair was recorded.

Egg production was calculated as the number of eggs laid per female during its highest peak, i.e. from the 5th. day up to the 10th. day of her life. Results obtained for lifetime egg production in the initial population (TANTAWY and RAKHA 1964) indicated that females lay most of their eggs during this period. Therefore, in each selected line, at a particular generation of selection the same flies which were measured for wing length were also measured for thorax length, longevity and

egg production.

A control stock was maintained under similar environmental conditions and the four different characters, as in the inbred lines, were examined.

Crosses between the selected inbred lines

Crosses between the four different lines, i.e. large (L) lines of A and B, and the small (S) lines of C and D were carried out at nearly 25, 50 and 75 percent coefficients of inbreeding. Six different crosses were carried out (LA X LB, LA X SC, LA X SD, LB X SC, LB X SD and SC X SD) and in each cross twenty random pair matings were used (males were used from the first line in each cross); eggs were counted for five successive days and cultured in well yeasted vials. Twenty pairs of flies were measured from the F_1 progeny, ten pairs on each of two days, An F_2 generation was also obtained from which twenty pairs were used. At each level of inbreeding wing length, thorax length, egg production and egg viability in the parental, F_1 and F_2 generations were estimated as before.

2. Outbreeding matings

Four different selected lines two plus (A', B') and two minus (C' , D') were established from the original foundation population. Each selected line was maintained by

measuring 60 pairs of flies in three sublines of a, b and c. The three largest pairs in each subline were selected and a cyclical system of mating was used as shown by TANTAWY et al (1964). Such a type of mating minimize the inbreeding, ROBERTSON and REEVE (1952b). This system was carried out for ten generations; in each generation the three extreme males and females from each subline within the selected strain were mated together to perform the new separate line.

Wing length, thorax length, longevity and egg production in each of the selected lines were determined at the 1st., 3rd., 6th. and at the 9th. generations of selection. Also a control population was maintained with the outbred selected lines and given the same treatments. The technical procedure in the study of the correlated traits was exactly as that done in the selected inbred lines, apart from the differences in relationship.

c. Heritability estimates in the selected lines

In both systems of mating, one selected line in each direction (i.e.,lines A, C and A', C' of the inbred and the outbred selected ones, respectively) was used to estimate the heritability of each of the characters studied. Progeny tests were carried out at the 1st., 3rd., 6th. and at the 9th.

generations of selection. The progeny resulting from the one hundred flies in each of A, C, A' and C' lines used in the study of the correlated characters were raised to obtain their F_1 generation. From each parental pair matings 10 pairs of flies from the F_1 were measured for wing and thorax length after which matings were made at random, five pairs being kept in an oviposition vial. Egg production was determined in the period from the 5th. day up to the 10th., while the death rate was calculated throughout the flies lifetime. These data allow us to measure the heritability of each character in the selected lines by doubling the phenotypic correlation between mothers and daughters as before.

d. Percentage of emergence

In all the selected lines at each generation, as well as in the crosses between the selected lines, records were kept of the number of eggs cultured per vial and the number of adults which hatched.

All the experimental work reported in the present investigations were carried out at $25 \pm 0.50^{\circ}$C.

RESULTS

Various characters in the initial foundation population

The absolute means for each of the characters studied in the base population, their coefficients of variation and heritability estimates are presented in Table 1. The results indicate clearly that the metric characters possess higher heritability estimates and lower variability than fitness ones and also demonstrate an inverse relation between heritability and phenotypic variation.

The genetic correlations (Table 2) indicate a high correlation between wing and thorax; with lifetime egg production the correlations are very low; with longevity the values are intermediate. The highest total phenotypic correlation is between longevity and egg production - hardly surprising - followed by the value between wing and thorax length. The results are in agreement with those reported by different authors, e.g. ROBERTSON and REEVE (1952b); REEVE and ROBERTSON (1953); TANTAWY (1959) working on wing length and Thorax length and ROBERTSON (1957b) on egg production in Drosophila melanogaster. TANTAWY, MALLAH and TEWKIK (1964) reported similar results for wing and thorax length in Drosophila melanogaster and D. simulans derived from the same locality as of the present study. MAYNARD SMITH (1959)

found that the heritability of longevity in Drosophila subobscura to be about 30 percent, calculated from his data by doubling the correlation between mothers and daughters.

Table 1. Means and coefficients of variation[°] (C.V.) for wing length, thorax length (1/100 mm), longevity (days) and lifetime egg production (average per female); heritability estimates in the initial population are also presented

Characters	Means[°°]	C.V.	Heritability[°°°]
Wing length (W)	189.75	3.07	0.2462
Thorax length (T)	96.25	3.83	0.2034
Longevity (L)	14.43	30.22	0.1129
Egg Production (G)	389.50	60.12	0.0257

° Sexes averaged

°° Each mean is based on 200 flies

°°° d. f. = 380

Table 2. Total phenotypic (r_P) and genetic (r_G) correlations between different characters

Correlations° between	r_P	r_G
W - T	0.5775 ± 0.116	0.7913
W - L	0.2197 ± 0.138	0.4025
W - G	0.2440 ± 0.137	0.0252
T - L	0.3315 ± 0.133	0.4013
T - G	0.5055 ± 0.112	0.0387
L - G	0.7568 ± 0.137	0.0557

° For symbols see Table 1

Response to selection for the primary character

The response to selection for wing length in plus and minus directions for both brother-sister and outbreeding are presented in Figure 1a and 1b as percentage deviations from controls. The results indicate clearly that both systems are effective in separating the initial population; selection for short wing length is more effective. In the case of sibs, selection is effective up to the third generation after which the selected lines are more or less constant, while the outbred selected lines show continuous response up to the tenth generation.

When selection was relaxed at different generations, the systems behaved differently. The selected inbred lines returned to the control level at lower coefficients of inbreeding while at higher coefficients relaxed selection led to no change. The outbred selected lines tend to return at the earlier generations to the control level while at the later generations relaxed lines returned half way. These results are in agreement with those reported by different authors working on similar experiments; for review see TANTAWY, MALLAH and TEWFIK (1964).

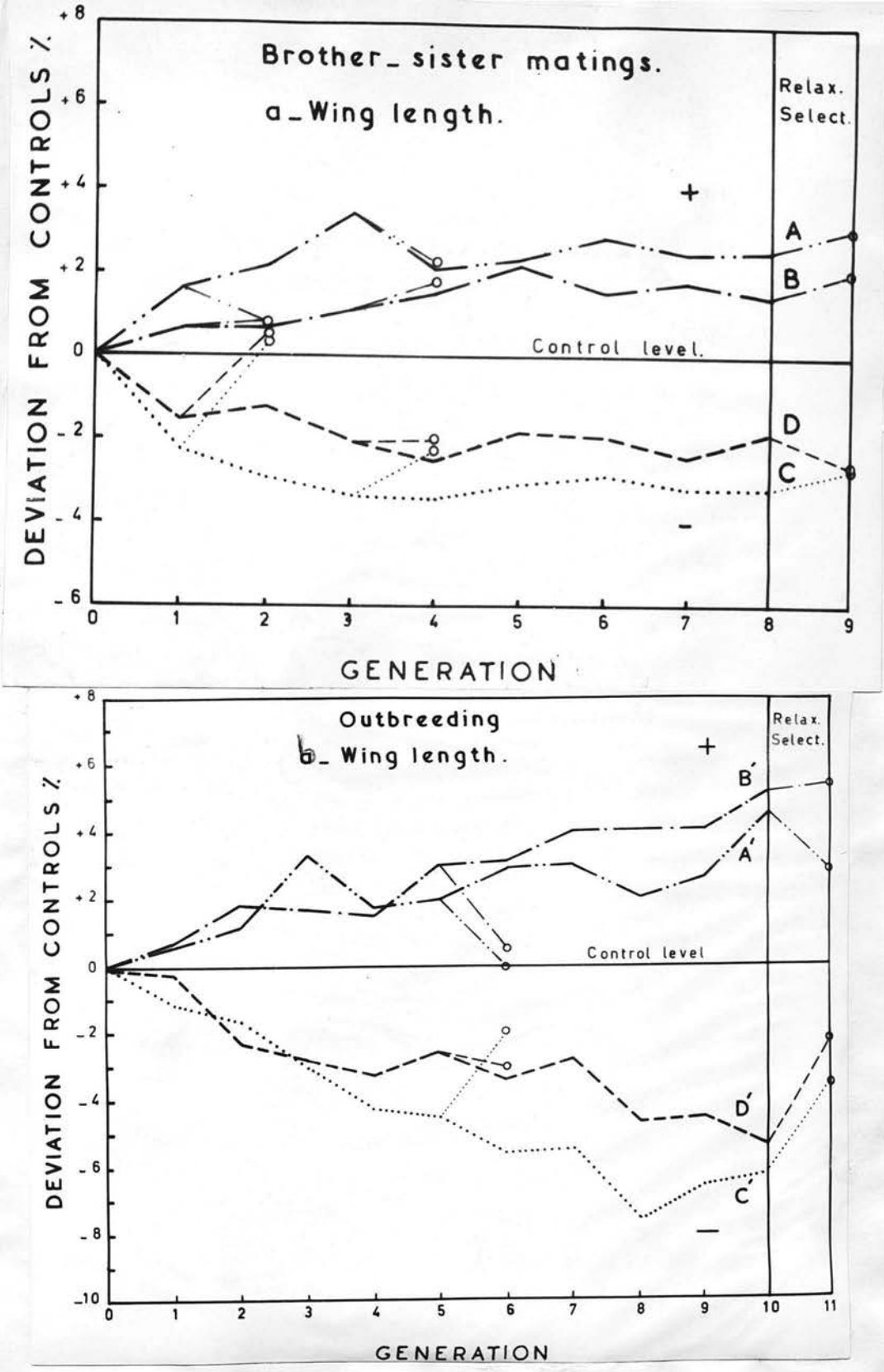


Figure 1. Response to selection in wing length (as a primary character) presented as percentage deviations from controls.

a. Brother-sister

b. Outbreeding

Correlated response to selection

The effects of selection on the other three characters, i.e. thorax length, longevity and egg production are shown in Figure 2. Since both lines, in each direction of selection within each system of mating, behaved almost identically, the plus or minus selected lines have been averaged and the results are presented as percentage deviations from controls. The results indicate clearly that thorax length shows a response to selection similar to that reported for wing length indicating a high genetic correlation between them (Table 2). The inbred and the outbred selected lines for wing length tend to show that flies with longer wing length live significantly ($P < 0.05$) longer than those selected for short wings. The correlated response to selection is more pronounced in the plus than in the minus direction; this is contrary to what was found in wing or thorax length.

The results for egg production indicate that selection for wing length causes the selected lines to diverge also in their capacity for laying eggs. Plus and minus inbred selected lines particularly at the higher levels of inbreeding, show significant decrease in egg production compared with the controls although long wing selected lines lay more eggs than those selected for short wings. The outbred selected

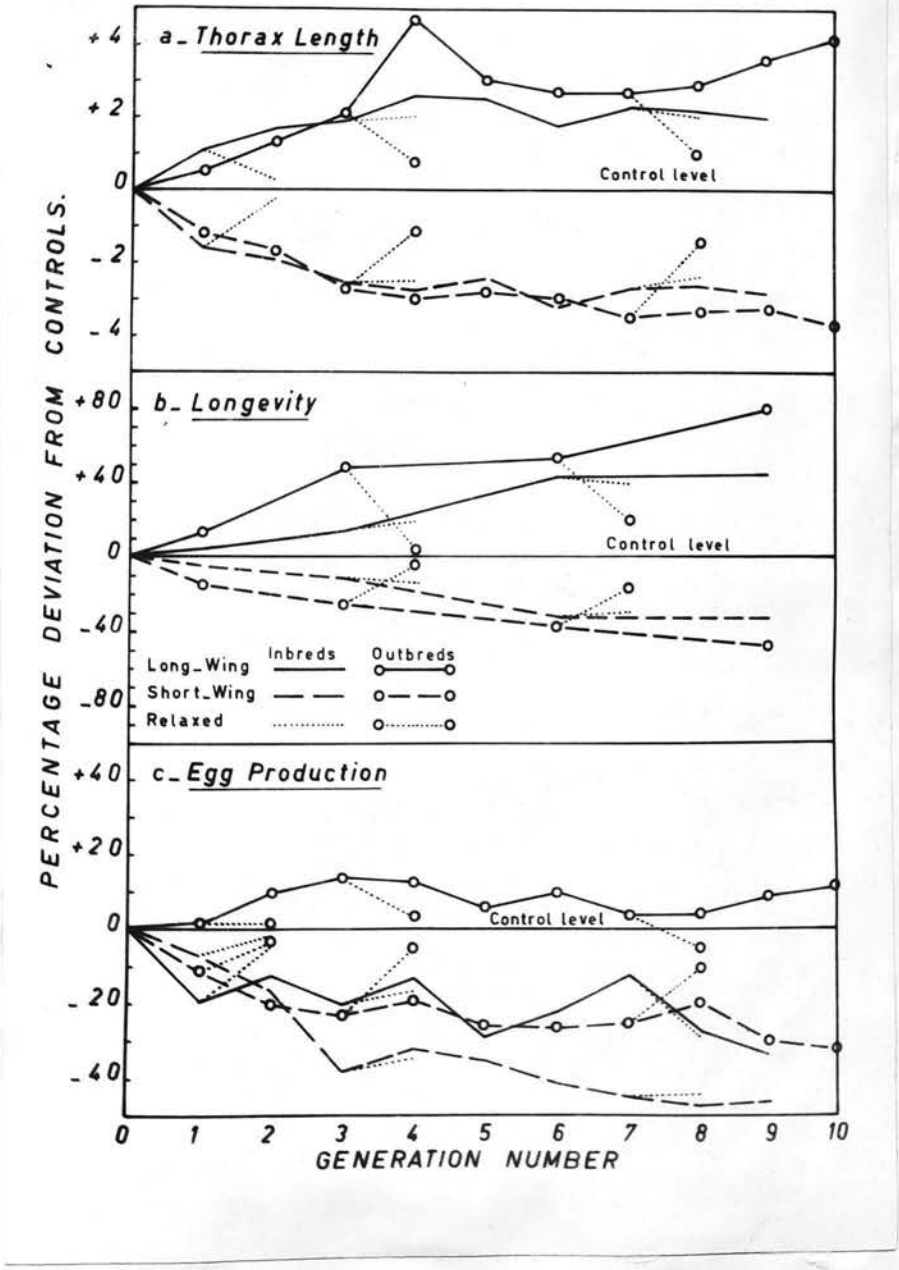


Figure 2. Response to selection for the correlated characters presented as percentage deviations from controls.

lines differ from those of sib matings since the long wing outbred selected lines lay more eggs than the controls, but the difference is not statistically significant while the short wing lines laid significantly ($P < 0.05$) fewer eggs than the controls.

The effects of relaxed selection on the secondary characters are similar to those found in wing length. There is apparent fixation of genes affecting different characters inthe selected inbred lines particularly at the higher levels of homozygosity. The outbred selected lines returned back half way to the control level. These results indicate that the inbred and the outbred selected lines behaved differently for all the characters studied.

Heritabilities and genetic correlations in the selected lines

Heritability, due to additive gene effects for a given trait, was estimated in both systems of mating by progeny tests carried out at the 1st., 3rd., 6th. and at the 9th. generations of selection. Due to the great labour involved, only one line in each direction of selection in each system of mating was used. The results of the heritability estimates (doubling the correlation between mothers and daughters) for all the characters studied are presented in Table 3, which indicate clearly that inbreeding with sibs

is a major factor in eliminating heterozygosity, i. e. the genetic variance, particularly at the higher levels of inbreeding. These results agree fairly well with those reported by TANTAWY and REEVE (1956) and TANTAWY (1959) on other populations of Drosophila melanogaster. On the other hand, the outbred selected lines behaved differently; heritability estimates do not change although there is a tendency for an insignificant increase as compared with the values of the initial populations. In both systems of mating minus selected lines show a tendency to display somewhat greater genetic variance than the plus ones. Such results confirm those reported by REEVE and ROBERTSON (1953) working on D. melanogaster and by TANTAWY, MALLAH and TEWFIK (1964) on D. melanogaster and D. simulans.

The genetic correlation between pairs of characters is presented in Table 4. The genetic correlations, in general, tend to decrease with increasing homozygosity. In the outbred selected lines genetic correlations tend to increase slightly over the levels of the foundation population. In both systems of mating, short wing selected lines display higher values than long wing ones. Similar results were given by ROBERTSON and REEVE (1953) for the outbred selected lines and by TANTAWY (1959) for the inbred ones.

Table 3. Heritability estimates in the primary and correlated characters at different generations of selection

Generations	Brother-sister		Outbreeding	
	+	-	+	-
a. Wing length				
1	0.213±0.054	0.224±0.059	0.254±0.054	0.278±0.056
3	0.185±0.011	0.189±0.034	0.285±0.073	0.314±0.082
6	0.053±0.037	0.061±0.053	0.291±0.079	0.299±0.075
9	0.039±0.028	0.042±0.045	0.314±0.067	0.328±0.063
b. Thorax length				
1	0.235±0.063	0.227±0.054	0.262±0.054	0.274±0.059
3	0.214±0.055	0.218±0.049	0.300±0.061	0.302±0.070
6	0.095±0.061	0.120±0.081	0.294±0.072	0.324±0.069
9	0.049±0.050	0.085±0.073	0.305±0.084	0.318±0.072
c. Longevity				
1	0.134±0.052	0.132±0.064	0.187±0.082	0.194±0.074
3	0.101±0.063	0.121±0.057	0.153±0.073	0.184±0.059
6	0.085±0.040	0.083±0.049	0.143±0.065	0.153±0.075
9	0.002±0.035	0.014±0.043	0.147±0.059	0.158±0.063
d. Egg production				
1	0.095±0.054	0.089±0.047	0.120±0.037	0.127±0.053
3	0.088±0.049	0.082±0.045	0.101±0.094	0.135±0.075
6	0.054±0.074	0.071±0.061	0.095±0.081	0.114±0.076
9	0.005±0.089	0.009±0.059	0.110±0.076	0.123±0.064

Table 4. Genetic correlations between different characters in the selected lines at various generations.

Generations and correlations	Brother - sister		Outbreeding	
	+	-	+	-
Generation 1				
W - T	0.8874	0.8607	0.9381	0.9265
W - L	0.4005	0.3768	0.4105	0.4007
W - G	0.0688	0.0076	0.0984	0.0075
T - L	0.3981	0.3652	0.3817	0.4120
T - G	0.0474	0.0399	0.0517	0.0732
L - G	0.0497	0.0399	0.0517	0.0732
Generation 3				
W - T	0.8543	0.8001	0.8947	0.9451
W - L	0.3514	0.3017	0.4267	0.4056
W - G	0.0674	0.0066	0.0095	0.0093
T - L	0.3014	0.2906	0.3987	0.3776
T - G	0.0148	0.0094	0.0157	0.0214
L - G	0.0331	0.0297	0.0581	0.0476
Generation 6				
W - T	0.7956	0.7652	0.9508	0.9357
W - L	0.3094	0.2741	0.4717	0.4067
W - G	0.0189	0.0053	0.0149	0.0098
T - L	0.2971	0.2540	0.4311	0.3998
T - G	0.0054	0.0057	0.0247	0.0097
L - G	0.0343	0.0412	0.0592	0.0501

Table 4. Cont.

Generations and correlations	Brother - sister		Outbreeding	
	+	-	+	-
Generation 9				
W - T	0.7143	0.7013	0.9413	0.9641
W - L	0.2811	0.2564	0.4798	0.4081
W - G	0.0097	0.0009	0.0195	0.0093
T - L	0.2541	0.2208	0.4352	0.3849
T - G	0.0022	0.0041	0.0347	0.0213
L - G	0.0211	0.0139	0.0611	0.0514

° For symbols see Table 1

Coefficients of variation in the selected lines

Phenotypic variances for wing and thorax lengths are calculated as coefficients of variation in order to minimize the effects of change in the mean size on variance. It was found that males and females have nearly the same coefficients of variation (Table 1) so that their coefficients have been averaged. The results are presented in Figure 3a and 3b which indicate that inbreeding is accompanied by a decrease in the phenotypic variance of wing length, compared with the controls, until wing length reached the selection limits. Selection with outbreeding did not change variability.

Thorax length as a correlated character behaves almost exactly like wing length. The phenotypic variability of longevity and egg production (results are not included) also indicate that inbreeding causes a decline and outbreeding an increase in variance.

Expected responses to selection

The expected responses to selection for the different primary and correlated characters studied were calculated by comparing, at a given generation, the selection differentials in units of the phenotypic standard deviation, heritabilities and the genetic correlation between the primary and the secondary concerned character. The statistical analyses were

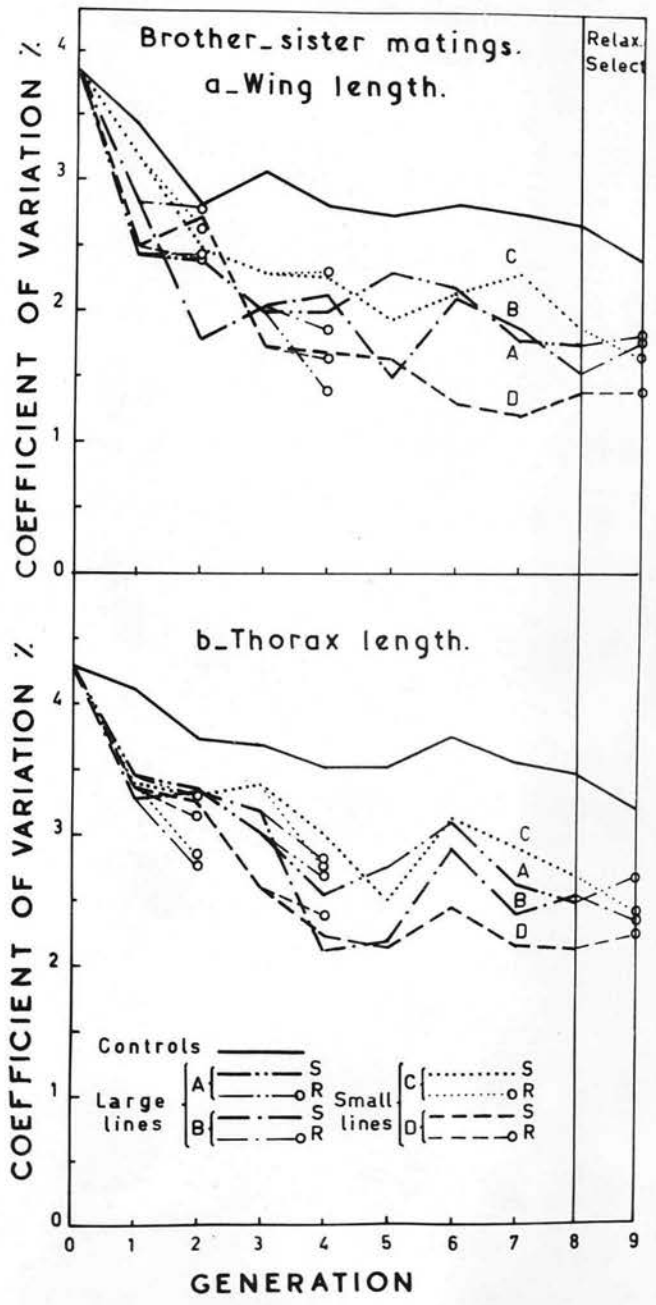


Figure 3a. Coefficients of variation for wing and thorax lengths in different selected inbred (brother-sister) lines.

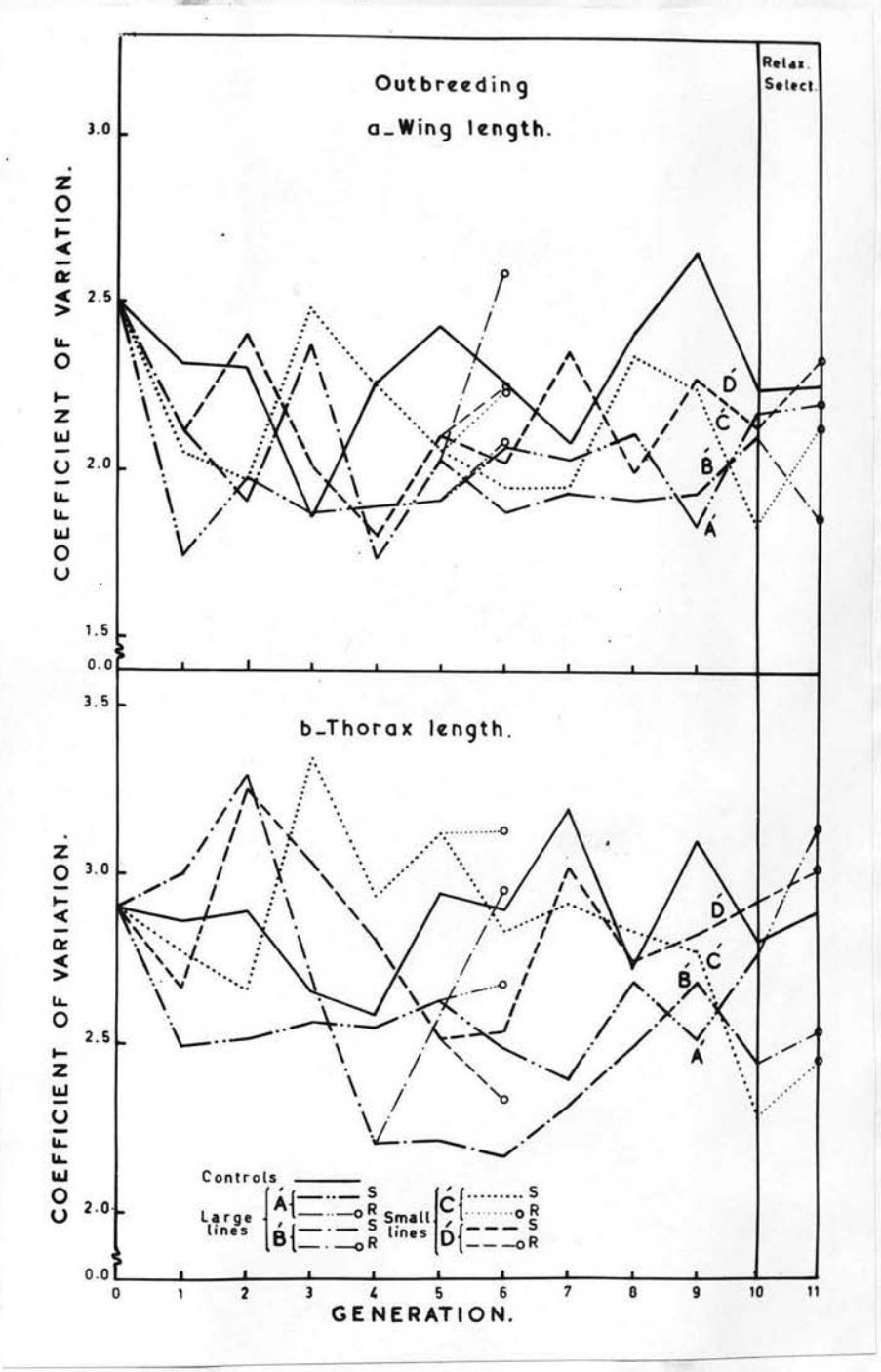


Figure 3b. Coefficients of variation for wing and thorax lengths in different outbred selected lines.

were exactly as reported by FALCONER (1960). The results, presented in Table 5, indicate, in general, good agreement in the outbred selected lines between the expected and the observed responses to selection for wing and thorax lengths. On the other hand, fitness characters show higher observed responses than expected.

The inbred selected lines behave differently since the expected responses to selection do not agree with the observed ones at higher levels of inbreeding even with metric traits due to increased homozygosity. Close agreements between observed and expected responses to selection cannot be expected, with characters of very low heritabilities. With low genetic correlations the expected response is small and liable to be obscured by random drift (CLAYTON, KNIGHT, et al 1957).

Table 5. Observed and expected responses to selection in the primary and secondary characters in the A, C inbred lines and the A', C' outbred selected lines

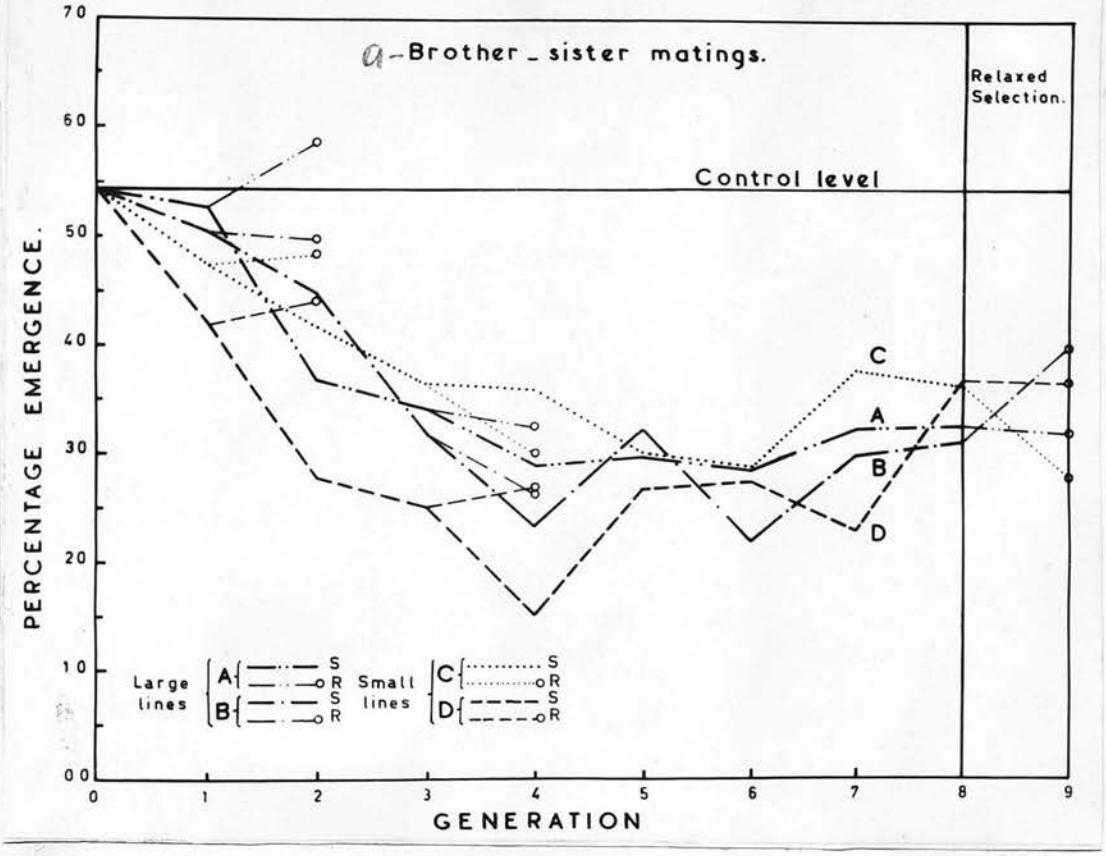
Generations	Brother - sister				Outbreeding			
	+		-		+		-	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
a. Wing length (1/100 mm, sexes averaged)								
1	0.950	1.039	-1.204	-1.342	1.846	1.891	-2.022	-2.041
3	5.882	0.561	-5.784	-0.915	6.331	6.011	-5.845	-5.731
6	5.990	0.145	-6.679	-0.190	5.424	5.139	-10.582	-10.189
9	5.108	0.078	-6.908	-0.125	6.906	6.842	-12.273	-12.051
b. Thorax length (1/100 mm, sexes averaged)								
1	0.904	0.939	-1.083	-1.197	1.637	1.861	-1.649	-1.898
3	2.134	0.483	-2.675	-0.838	5.741	5.833	-4.897	-5.020
6	1.909	0.149	-3.427	-0.212	5.106	4.827	-9.842	-10.086
9	2.083	0.061	-3.502	-0.127	6.531	6.494	-10.884	-11.118
c. Longevity (days, sexes averaged)								
1	2.243	0.310	-1.419	-0.412	4.507	0.681	-2.816	-0.699
3	2.459	0.125	-1.951	-0.256	6.084	1.786	-4.609	-1.871
6	3.167	0.050	-2.145	-0.069	6.763	1.463	-5.113	-3.438
9	3.420	0.002	-2.762	-0.021	7.949	1.910	-6.708	-4.010
d. Egg production (average per female per day)								
1	-2.654	0.005	-4.237	-0.058	1.705	0.010	-4.994	-0.136
3	-2.635	0.003	-9.283	-0.047	2.321	0.033	-6.263	-0.036
6	-4.137	0.001	-10.781	-0.004	5.217	0.029	-11.064	-0.094
9	-5.959	0.001	-12.049	-0.002	5.128	0.038	-13.261	-0.144

Percentage of emergence

The percentage of emergence was calculated as the number of flies that hatched from a given number of eggs. The results in all the selected lines are presented in Figure 4a and 4b. It is clear that inbreeding is effective in decreasing the percentage of emergence in all the selected lines up to the third generation after which it ceased to decrease. The outbred lines show, though less effects on percentage of emergence than in the inbreds, a gradual decrease was observed in this character; low lines are more viable than the high ones.

Relaxation of selection causes no effects in the inbred lines particularly at the higher levels of homozygosity, while in the outbred lines relaxation of selection causes percentage of emergence to return back to the control level.

The above results agree with those reported by ROBERTSON and REEVE (1953); TANTAWY (1956, 1959) on Drosophila melanogaster, by TANTAWY, MALLAH and TEWFIK (1964) on D. melanogaster and D. simulans and by PREVOSTI (1955) on D. subobscura.



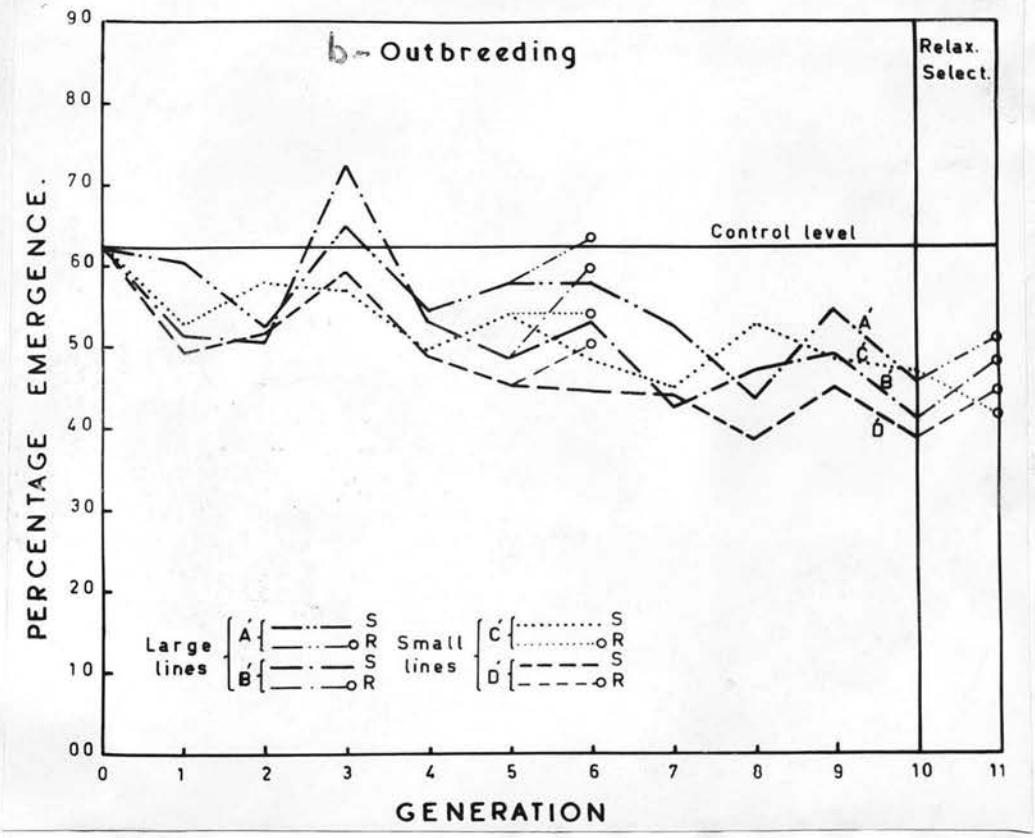


Figure 4. Percentage of emergence in the different selected lines. a. Brother - sister, and b. Outbreeding.

Crosses between selected inbred lines

The four different selected inbred lines (large A and B; small C and D) were crossed together at the first, third and at the seventh generations of selection, i. e. at the levels of 25, 50 and 75 percent coefficients of inbreeding, to study the percentage of heterosis in wing length as well as in the different correlated characters. The dominance ratio for only wing length and thorax length was calculated when the response to selection had ceased (ROBERTSON and REEVE 1955).

Percentage of heterosis

Percentage of heterosis has been estimated in the F_1 and F_2 generations as percentage deviation from the mid-parent value as suggested by ROBERTSON and REEVE (1955) and TANTAWY (1957). The results are presented in Table 6, from which the following points emerge; for the percentage of heterosis in wing, thorax lengths and egg production.

a. Percentage of heterosis increases with increasing homozygosity; the highest values are shown at 75 percent. There is a break down in the level of heterosis in the F_2 generation.

b. When the long wing selected lines were crosses, the F_1 generation does not differ significantly from their mid-parent level, although there is a tendency for a positive

deviation.

c. In crosses between small body size there is a general tendency for the percentage of heterosis to be higher than in crosses between long wings lines.

d. Crosses between selected inbred lines of different body sizes lead to greater heterosis than between lines of similar sizes.

Fitness characters, i.e. egg production and egg viability are more affected by crossing than metric ones. Table 6 also shows that the F_1 hybrids particularly at the higher levels of inbreeding produce higher number of eggs per day than the parental lines. There is always a breakdown in heterosis in F_2 generation. The results also suggest that crosses between lines of different body sizes give higher heterosis than those of similar sizes.

Egg viability is considered to be the most heterotic character (TANTAWY 1957) and there are different proportions of heterosis percentage in the various crosses between different inbred lines. These results are expected because of the great effects of selection and inbreeding (Figure 4a,b) on such a character. Significant decrease in the percentage of emergence are particularly clear at the higher levels of inbreeding and when the inbred lines are crossed the F_1 progeny

Table 6. Percentage of heterosis resulting from crosses of the various selected lines at different levels of inbreeding. Crosses were made between long (L) wing lines and short (S) wing lines as well as between long x short wings.

Coefficients of inbreeding	25%		50%		75%	
Crosses	F_1	F_2	F_1	F_2	F_1	F_2
a. Wing length						
L x L	-0.61	0.96	1.08	0.43	0.99	0.76
L x S	0.90	1.12	2.29	1.48	2.37	1.39
S x S	1.25	0.67	0.71	0.11	1.25	1.01
b. Thorax length						
L x L	0.74	0.56	1.17	0.59	1.62	0.21
L x S	0.57	0.48	1.78	1.09	1.89	0.81
S x S	2.61	1.78	2.83	1.73	1.44	0.83
c. Daily average egg production						
L x L	11.89	3.68	3.91	3.37	17.11	8.37
L x S	12.63	1.48	22.95	12.32	47.00	20.00
S x S	-3.94	9.54	19.19	14.16	26.23	17.12
d. Percentage of emergence						
L X L	-4.75	-1.31	90.03	47.57	135.03	103.40
L x S	4.56	-2.95	55.82	39.46	93.07	71.55
S x S	4.01	2.72	45.48	33.61	54.03	41.45

display greater heterosis. Again we find a positive correlation between the extent of inbreeding and the magnitude of heterosis.

Phenotypic varaition in the crossed inbred lines

Phenotypic variation of wing and thorax length measured as coefficients of variation are presented in Table 7, for the parental, F_1, F_2 generations and also for the controls. Variations of egg production and of egg viability (results are not presented) behave in a similar way as wing length but show much higher variability.

The results , presented in Table 7, indicate that the F_1 generation is generally, but not always, less variable than the parental generation, while the F_2 shows insignificantly higher variability than the parental generation. The results suggest that environmental variance is not constant for all genotypes and tends to be smaller in heterozygous individuals than homozygotes. Such results agree with those reported by ROBERTSON and REEVE (1952a) on Drosophila melanogaster and MAYNARD SMITH (1959) on D. subobscura.

Table 7. Coefficients of variation for wing and thorax lengths in the controls, mid-parent (M.P.) and in the different crosses between the various selected lines (sexes averaged) at different levels of inbreeding.

Crosses	25%			50%			75%		
	M.P.	F_1	F_2	M.P.	F_1	F_2	M.P.	F_1	F_2
a. Wing length									
Controls	3.43	3.09	2.82	3.09	2.76	2.83	2.79	2.43	2.47
L x L	2.64	2.91	2.81	2.02	1.68	1.62	1.85	1.59	1.69
L x S	2.72	2.52	2.44	2.02	1.54	2.28	1.80	1.54	2.02
S x S	2.84	2.05	2.24	2.12	1.38	2.35	1.76	1.37	2.26
Averages for crosses	2.73	2.49	2.50	2.05	1.53	2.08	1.80	1.50	1.99
b. Thorax length									
Controls	4.12	3.68	3.52	3.68	3.52	3.76	3.56	3.20	3.17
L x L	3.37	3.13	3.68	3.10	2.39	2.19	2.51	1.87	2.06
L x S	3.38	2.95	3.40	3.05	2.44	3.30	2.52	2.19	3.18
S x S	3.40	2.88	2.54	2.99	2.00	2.75	2.54	2.09	2.78
Averages for crosses	3.38	2.99	3.21	3.05	2.28	2.75	2.52	2.05	2.67

Dominance ratio in the crossed inbred lines for wing and thorax lengths

ROBERTSON and REEVE (1955) estimated the dominance ratio for body size in Drosophila melanogaster after crossing various selected inbred lines; crossing was carried out when the selection limits had been achieved. Table 8 summarises the results of the different crosses between various selected lines of different body sizes at the 8th. generation. There is a considerable differences in size between parents and it is, therefore of great interest to examine the position of the F_1 generation with regard to the parent and mid-parent sizes. Table 8 shows the size differences between parents ($P_1 - P_2$) where P_1 is the larger parent, the absolute deviations (F_1 - M.P.) and the dominance ratio as suggested by ROBERTSON and REEVE (1955). The ratio will be one for complete dominance and zero for strict intermediacy.

It is clearly shown from the results presented in Table 8 that there is a higher degree of dominance ratio for wing length in crosses between large x small for the large line A than for line B. Crosses between lines of similar body size (large x large or small x small) suggest complete dominance for wing length and thorax length. The various crosses suggest that the F_1 generation is never below the mid-parent level, and there is a considerable departure of the F_1

from the strict intermediacy in favour of the larger parent. These results agree fairly well with those reported by ROBERTSON and REEVE (1955).

CONCLUSIONS

The experiments confirm and extent the results of similar studies carried out by various investigators, e.g. ROBERTSON and REEVE (1952b); TANTAWY (1959); TANTAWY, MALLAH and TEWFIK (1964) working with wing length in Drosophila melanogaster, and DRUGER (1962) with Drosophila pseudoobscura.

The salient features include:

1. Selection for short wing is more effective than selection for long wing length.
2. Selection response is curtailed by inbreeding.
3. Fraction due to inbreeding consequent on selection, is reflected in the stability of the mean when selection is relaxed both for the primary character selected and also other characters which show different degrees of correlated change. As expected there is a high correlation between wing and thorax length, since both reflect changes in body size.

There is evidence that lines selected for long wings live longer which is not anticipated. In outbred lines, egg production is virtually unchanged by increase in wing length,i.e. body size, confirming the evidence of ROBERTSON (1957a), but there is an association with body size since the smaller flies lay fewer eggs. This may well be due to the higher levels of homozygosity in lines selected for small size and therefore the

apparent correlation may be rather indirect and complex in origin compared with say, the simple correlation between wing and thorax length.

Comparing the apparent genetic correlation in the base population with the effects of selection, we find greater correlated change in longevity than expected and the same is true for egg production in the small lines, for the probable reason just noted.

Crossing between selected inbred lines follow the same pattern as that reported by ROBERTSON and REEVE (1955). Heterosis is generally highest in crosses between lines which show the greatest reduction below the normal level and this is clearly associated with the return to the highly heterozygous gene arrays which occur in the wild population.

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SUMMARY

1. The experiments were designed to examine correlated changes in thorax length, longevity and egg production when wing length in Drosophila melanogaster was selected for. Two different mating systems were used: brother - sister mating x

outbreeding and for each system selected plus and minus lines were maintained.

2. Heritability was estimated in the unselected base population; and was found to be 0.25, 0.20, 0.11 and 0.03 for wing length, thorax length, longevity and egg production, respectively.

3. The inbred lines failed to respond further after three generations of selection, while the outbred lines were still responding when the experiment was stopped in the tenth generation.

4. When selection was relaxed, the inbred lines hardly changed, especially at higher levels of homozygosity, while the outbred lines always returned to the control level.

5. Selection for wing length was accompanied by change in the other three characters. Thorax length showed a closely similar proportional change to that of wing length; flies selected for larger wing length lived longer while egg production was reduced in short wing lines; otherwise no change took place.

6. The different inbred lines were intercrossed at 25, 50 and 75 percent coefficients of inbreeding and the percentage of heterosis was determined for the F_1. This increased as the level of homozygosity increased and there was also a decline in the F_2 below the F_1 level.

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