

Inversion heterozygosity and selection for wing length in *Drosophila subobscura*

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(Received 7 February 1967)

1. INTRODUCTION

Drosophila subobscura, the most common indigenous species of *Drosophila* in Europe, has six elements in its caryotype: five rods with inversion polymorphism and one dot. The presence of inversion polymorphism in all the chromosomes, with the exception of the small dot, allows us to examine the possible heterotic effects of the heterozygosity in the blocks of genes constituting the inverted segments of the chromosomes. With this purpose, selection experiments were planned to determine the correlation between changes in the phenotype and the structure of the chromosomes in the selected lines. A preliminary paper (Prevosti, 1960) presented the data corresponding to two lines, one selected for long and the other for short wings. In the latter, homozygosity for one chromosomal arrangement was established in the five chromosomes after nine generations of selection. The line was derived from a highly polymorphic population. On the other hand, in the line selected for long wings, the polymorphism was preserved and indications of heterotic effect were found in the heterozygous combinations of some of the chromosomal arrangements.

Since then other lines have been analysed, while our knowledge of polymorphism in the natural populations of this species has been considerably enlarged (Knight, 1961; Sperlich, 1961, 1964; Kunze-Mühl & Sperlich, 1962; Sperlich & Kunze-Mühl, 1963; Pentos-Daponte, 1964; Krimbas, 1964 *a, b*; Prevosti, 1964 *a, b*, 1966 *a*). With this additional information it should be possible to shed further light on the significance of the chromosomal variation in the natural populations, and relate this to the results of the selection experiments. The data from the lines already analysed in the preliminary paper will be presented here in greater detail.

In the grasshopper, *Moraba scurra*, data about relations between inversion polymorphism and body size have been published by White & Andrew (1960, 1962) and by White, Lewontin & Andrew (1963), showing a relation between some chromosomal types and body weight. Also, the results obtained by Spiess & Schuellein (1956), Spiess (1958) and Spiess & Spiess (1964) in *D. persimilis* are of interest for the purpose of the present paper. The authors found a relation between development rate and two gene arrangements in the third chromosome. Since the rate of development may be correlated with body size (Robertson, 1963) these results may have some relevance to the data dealt with in the present paper.

2. MATERIAL AND METHODS

A sample of fifty females of a wild population of *D. subobscura*, from Barcelona (Spain), was used to start the population employed in the present experiments. From this population were derived four selection lines: two lines, one selected for long (B_1L) and the other for short wings (B_1S), were run in parallel with an unselected control line (B_1C). A further pair of lines, also selected for increase or decrease of wing length (B_2L and B_2S , respectively) were established independently and run with their own control line (B_2C). The whole experiment was thus replicated. The method of selection, as well as the technique of measuring the wing length and other details, were the same as in previous selection experiments (see Prevosti, 1956), in which however, the chromosomal types were not studied.

The frequencies of the chromosomal types in the initial population were determined in a sample of 132 males trapped in the wild and compared with the frequencies in the females used to start the selected lines. The results of this analysis and the procedure have been published (Prevosti, 1964*a*). After fourteen generations of selection for wing length the chromosomal types were determined in twenty-five males of the lines selected for short and in seventy males of the lines selected for long wings. The sample of twenty-five was found adequate in the short-wing lines, because of the high level of homozygosity reached in these lines. The tested males were crossed by single pair-mating with females of the Küssnacht stock which is homozygous for the standard orders in all the chromosomes. From the progeny of these crosses, seven larvae were analysed to ensure a high probability of observing both members of each pair of homologous chromosomes of the tested males.

The lines dealt with in the earlier paper were started from a sample of fifty females trapped in Pobla de Lillet, about 100 km. north of Barcelona. Selection was stopped and the chromosomal analysis carried out after only nine generations of selection. The Pobla de Lillet line selected for long wings will be called PL and the line selected for short wings PS.

3. RESULTS

(i) *Changes in wing length attained in the selected lines*

Figure 1 shows the results of fourteen generations of selection in the four lines analysed for chromosomal arrangements, as well as those obtained in the PL and PS lines. The figure also includes for comparison the results of other selection lines, obtained in earlier experiments (see Prevosti, 1956). One pair of these lines came from a Dalkeith population, in Scotland, and is referred to as DL and DS; the other pair came from a Kent population, in the South of England, and is referred to as KL and KS. Increase or decrease in wing length is measured as the difference between the mean of each selected line and that of the corresponding unselected control.

The response to the selection is clearly asymmetrical, being much greater when selection is for short wing length. In the B_1 and B_2 lines, where the selection has

been continued for longer than in the other lines, the asymmetry in the response increases during the later generations due to almost complete lack of response in B₁L and B₂L. The data in Table 1 show that the heritability is greater in the S lines than in the L lines from the beginning of the selection. Later the heritability drops

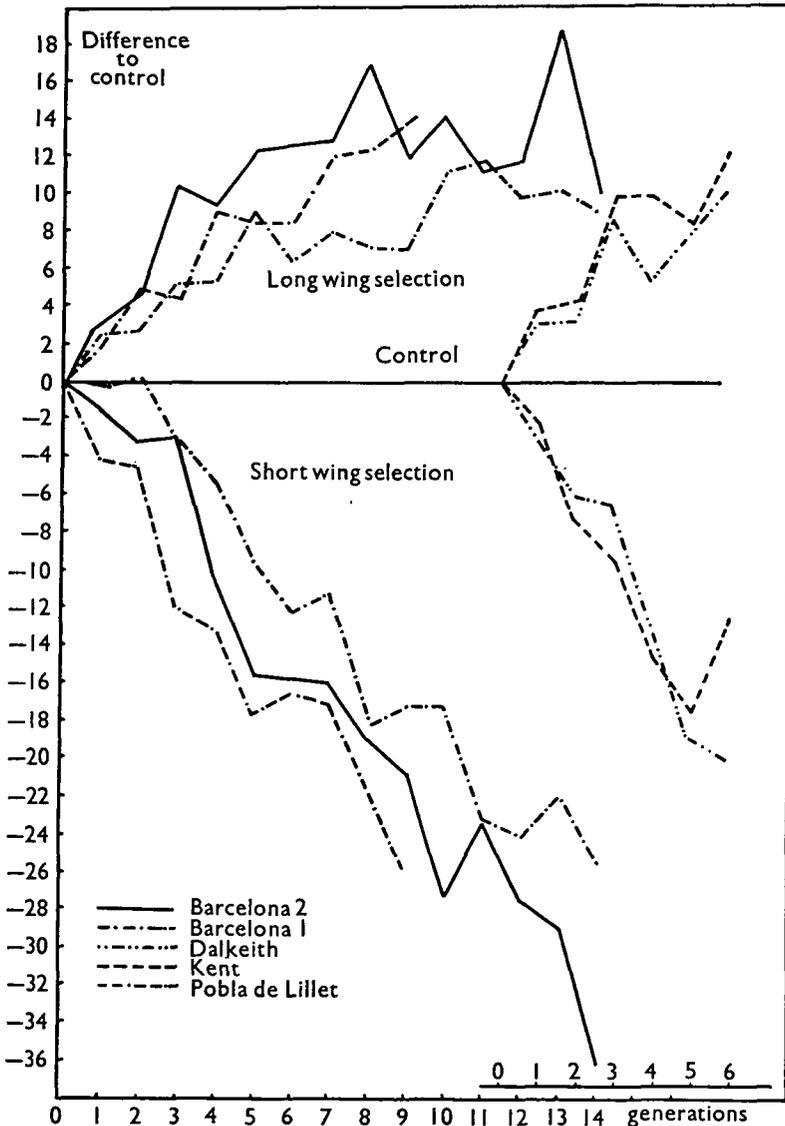


Fig. 1. Deviation of wing length (in micrometer units, one unit = 0.0152 mm.) from the control. The two sexes are averaged.

to zero in both BL lines, as can be deduced from the lack of response in the last generations of selection (Fig. 1), while the heritability is maintained in the S lines. Table 2 shows that the asymmetry in the response is due not only to the differ-

ences in heritability. The selection differentials are greater in the S lines, in spite of the uniform selection procedure in which the extreme 20% of flies with the longest or the shortest wings were selected. The differences in the selection differentials are apparently due to an asymmetrical distribution of wing length. In the earlier paper (Prevosti, 1956), where the data relating to the D and K lines were analysed, the asymmetry of the distributions of wing length was demonstrated and shown to be significantly negative.

The magnitude of the response is rather similar in all the lines studied. However, in the B₁ lines, the response is consistently lower than in the B₂ lines. This agrees with the lower heritability in the B₁ lines, which is probably due to lower genetic variance in these lines, since the coefficient of variability is also a little lower.

The gains obtained by selection are given as percentages of the mean of the control lines for corresponding generations in Table 3. These gains, specially in the short-wing lines, are rather high compared with those obtained in other experiments with

Table 1. *Realized heritability*

	Lines selected for long wings	Lines selected for short wings
Dalkeith (6 gen. sel)	0.23 ± 0.07	-0.41 ± 0.05
Kent (6 gen. sel)	0.33 ± 0.07	-0.31 ± 0.06
Pobla Lillet (6 gen. sel)	0.36 ± 0.10	-0.45 ± 0.09
Barcelona 1 (6 gen. sel)	0.21 ± 0.07	-0.51 ± 0.07
Barcelona 2 (6 gen. sel)	0.43 ± 0.07	-0.52 ± 0.07
Pobla Lillet (9 gen. sel)		-0.40 ± 0.04
Barcelona 1 (14 gen. sel)		-0.40 ± 0.03
Barcelona 2 (14 gen. sel)		-0.53 ± 0.03

The realized heritability has been estimated according to Falconer's method (1953) as the regression of the response to selection on the cumulated selection differential.

Table 2. *Average selection differentials per generation (in micrometer units: one unit = 0.015 mm.)*

	Long wing	Short wing
Dalkeith	6.40	9.13
Kent	6.23	7.71
Pobla de Lillet	4.40	6.48
Barcelona 1	4.18	5.05
Barcelona 2	4.65	5.33

Table 3. *Percentage deviation from unselected size at the end of the selection*

	Long wings	Short wings
Barcelona 1 (14 gen. sel)	5.20	14.66
Barcelona 2 (14 gen. sel)	6.43	22.90
Pobla Lillet (9 gen. sel)	8.56	15.70

a different species, i.e. in *D. melanogaster* by Robertson & Reeve (1952) using the same trait and a similar criterion of selection.

(ii) *The chromosome structure in the selected lines*

The wild population from which were derived the flies used to start the selection lines, shows considerable chromosomal inversion polymorphism. Table 4 gives the frequencies of the chromosomal types found in this population, in a sample of wild males trapped at the same time as the females which were used for starting the selection lines. The significance of this polymorphism has been discussed (Prevosti, 1964). Table 4 also presents the data relating to the chromosomal structure in the selected lines, and includes the already published data from the P lines (Prevosti, 1960). Since the data from the P lines were obtained by analysing the chromosomes in larvae of the selected lines, without crossing to the standard homozygous stock, only chromosomal orders in heterozygous combination could be detected. For this reason the figures corresponding to the P lines indicate only the frequencies of chromosomal orders detected in heterozygous combination.

A glance at the data in Table 4 reveals that in the short-wing lines selection leads to the fixation of one chromosomal order. Only in two chromosomes out of fifteen was fixation not demonstrated. An interesting feature of this fixation is that usually the same chromosomal orders are fixed in the different lines. Moreover, in no case has a chromosome with the standard order been fixed, in spite of the fact that, in the starting population, the standard order was the most frequent in three of the five polymorphic elements of the karyotype. Only in the J chromosome is the order fixed, J_1 , also the most frequent order in the starting population. The clear tendency to fixation of the same order in the three S lines eliminates the possibility of a predominant random factor in this fixation and it appears that when we select for short wings we are favouring genotypes homozygous for specific chromosomal orders.

Contrasting with the results obtained in the S lines, selection for long wings does not lead to fixation. Among fifteen possible cases only one chromosome has been fixed in the L lines, the O_{st} in the B_2L line. With this exception, a chromosomal polymorphism is maintained in these lines. But this polymorphism differs from that in the starting population. Selection for long wing length tends to develop a polymorphism which involves the standard order and the order fixed by selection for short wings. In spite of some exceptions the trend is clear, since it holds for eleven out of the fifteen chromosomes. Moreover, in most cases the frequency of both orders approaches 50%. The results obtained for the U chromosome are specially significant in this sense. In spite of the very low frequency of U_{st} (4.5%) in the starting B population, the frequency of this structural type approaches 50%, after selecting for long wings. So it appears that when we select for long wings we tend to select flies heterozygous for specific chromosomal arrangements which presumably exert a heterotic effect on wing size.

The results for chromosome J constitute a clear exception to the conclusion stated

Table 4. Frequency (%) of chromosomal types before and after the selection for wing length

Chromosome orders	Unselected population,* n = 132	Selected populations					
		Long wings**			Short wings**		
		B ₁ (n = 70)	B ₂ (n = 70)	P (n = 25)	B ₁ (n = 25)	B ₂ (n = 25)	P (n = 25)
A _{st}	51.5	58.4	42.9	40			
A ₁	6.0						
A ₂	42.4	41.6	57.1	40	100	100	100
J _{st}	29.3	17.1	28.6	28			
J ₁	70.7	83.9	71.4	28	100	100	100
U _{st}	4.5	38.5	45.7	32			
U ₁₊₂	48.4	7.1					
U ₁₊₂₊₈	45.4	54.4	54.3	32	100	100	100
U ₁₊₂₊₃	0.7						
U ₁₊₂₊₆	0.7						
E _{st}	35.5	40.0	61.4	64			
E ₁₊₂	24.4	10.0	38.6		24.0	100	
E ₁₊₂₊₉	13.3				76.0		
E ₁₊₂₊₉₊₁₂	19.2	50.0		52			100
E ₁₊₂₊₉₊₃	1.4						
E ₈	5.9			12			
O _{st}	38.3	60.0	100	52			
O ₃₊₄	20.3			44	100	84.0	100
O ₃₊₄₊₇	22.5	40.0		4			
O ₃₊₄₊₈	10.5						
O ₃₊₄₊₃	3.0						
O ₃₊₄₊₁	2.2						
O ₃₊₄₊₂₂	1.5						
O ₃₊₄₊₂₊₁₆	0.7						
O ₇	0.7						16.0

* This unselected population corresponds to the B lines.

** The figures for the P lines correspond to frequencies of chromosomal orders detected in heterozygous combination. The orders of the homozygous combinations were not tested.

in the last paragraph. In this chromosome it seems as if selection for long wings does not change the frequencies of the structural orders, since in the selected lines these frequencies are rather similar to those of the starting population. This could be connected with the shortness of the segment involved in the J_1 inversion, the only rearrangement found for this chromosome in Barcelona. Actually, the J_1 inversion is by far the shortest among all the inversions conserved in the L lines.

Comparing the data in Table 4 with the geographical distribution of the chromosomal arrangements (see Prevosti, 1964, 1966) we find that the chromosomal orders fixed in the lines selected for short wings are generally those most frequent in the southern populations, while the standard orders are most frequent in the north European populations (see Knight, 1961; Sperlich, 1964). Hence, the heterosis found in the long-wing lines rests on the heterozygous combination of chromosomal orders typical of the extreme north and south regions of the species distribution.

(iii) *The viability of the selected lines*

Both the selected and the control lines show considerable oscillations in viability

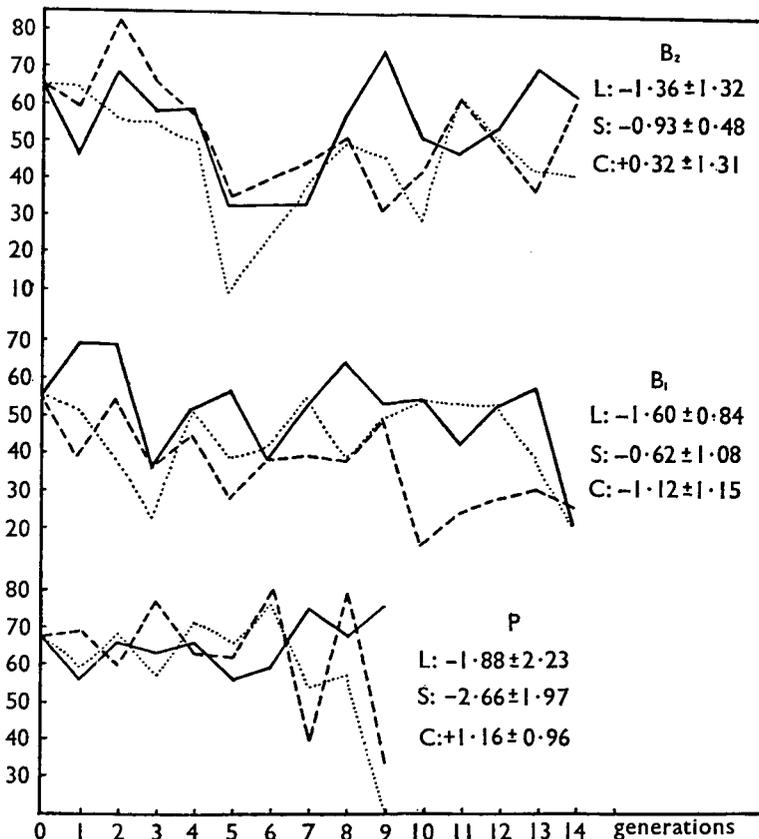


Fig. 2. Viability in the selected lines. The figures at the right are the regression coefficients of viability on generation number. Long-wing selection ----, short-wing selection ·····, unselected control ———.

(Fig. 2). These oscillations are attributable to a random occurrence of non-genetic influences difficult to control with the usual method of *Drosophila* culture, and hence the regressions of viability on selection generation are not statistically significant. However, it must be pointed out that this regression is negative in all the selected lines whether selected for long or short wings. On the other hand, it is positive in two cases and negative in one case in the control lines. The consistency of sign of the regression in the selected lines suggests that the progress of selection leads to a decrease in viability as is usually the case in artificial selection experiments. For the reasons just stated little can be said about the differences in viability between the different lines, except that if differences exist they are not very important.

(iv) *Variability in the selected lines*

The standard deviation of wing length in the selected lines does not show much change during the course of selection (Fig. 3). Only in the PS line is there a significant decrease, as expressed by the regression of the standard deviation on generation of selection. In the other selected lines this regression is usually negative, but not significantly so.

The coefficient of variability (Fig. 4) leads to the same conclusion: the regression on generation number is usually negative in the selected lines, in contrast with the control lines, but in no case is it significantly so. Hence individual variability does not change during selection or decreases only slightly.

4. DISCUSSION

The changes in the frequency of the chromosomal types observed in the selection lines could explain, at least in part, some of the features of the response to selection in these lines.

The dramatic responses obtained, compared with the results of other authors using the same selection criteria, could be explained in two ways. Firstly, the larger basis of genetic variability in the starting population could be involved. A sample of fifty females from a wild population was used to found the population, instead of a single pair of flies as by other workers. Secondly, numerous inversions were present. During selection the blocks of genes included in these inversions behave as 'supergenes' controlling differences in wing length, as the changes in the frequencies of the chromosomal types show. So, at least in the early generations—the period studied in this paper—selection is concerned with only a few units, each with a rather large effect. In other species, e.g. as *D. melanogaster*, which do not have numerous inversions on the chromosomes, selection acts on polygenic variation, i.e. units of small individual effect, which are only partially tied in groups by linkage. In this case, the long-term effects are probably greater, but the short-term effect will be less.

The asymmetry of the response to selection in opposite directions is a rather general result of this type of selection. Reeve & Robertson (1953) reported evidence

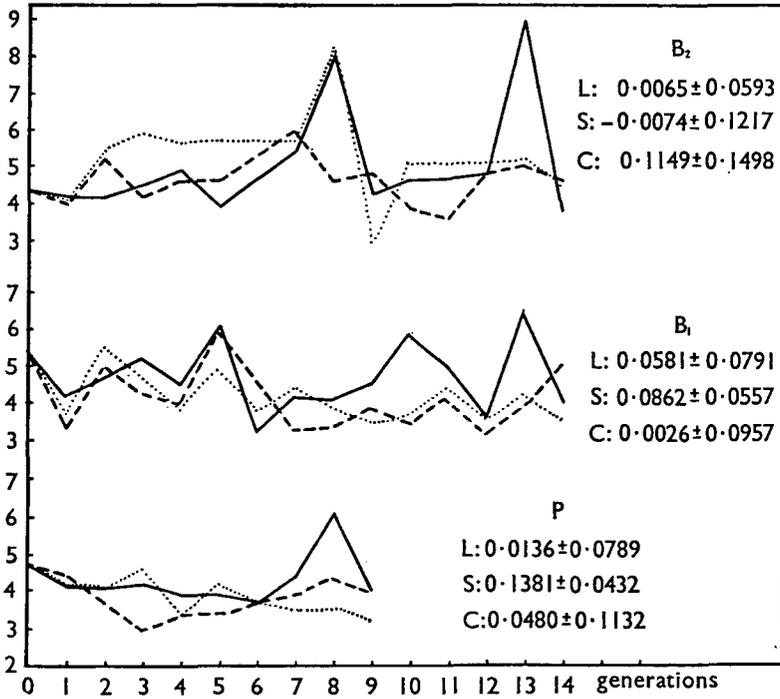


Fig. 3. The standard deviation (σ) of wing length in the selected lines. The figures on the right are the coefficients of regression of the standard deviation on generation number. Long-wing selection ----, short wing selection ·····, unselected control —.

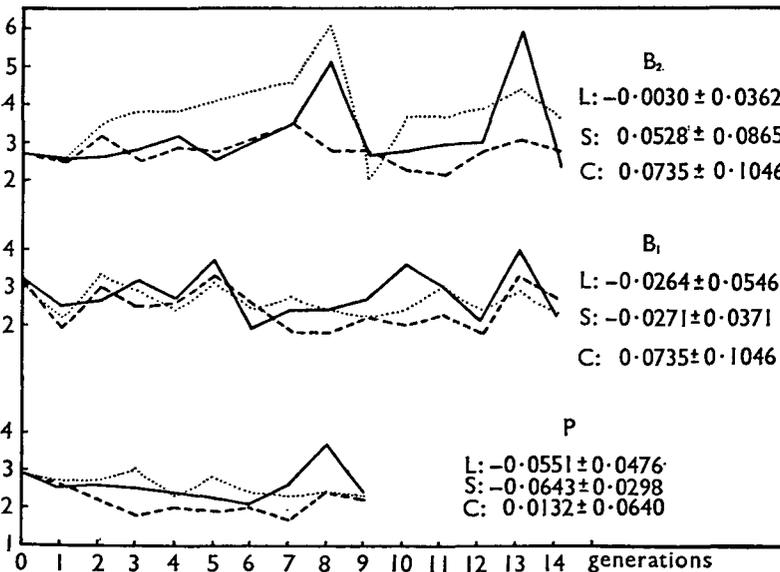


Fig. 4. The coefficient of variability (v) in the selected lines. The figures on the right are the coefficients of regression of v on the generations. Long-wing selection ----, short-wing selection ·····, unselected control —.

in their *D. melanogaster* selected lines of 'unstable genetic equilibrium maintained by selection for long wings'. They concluded that one of the elements contributing to the body-size changes in these lines consisted of genes or gene combinations with heterotic effect. Falconer (1953) believes that directional dominance is one of the main factors giving rise to asymmetrical responses. The data presented here agree with these interpretations. Directional dominance of long wings over short wings or superdominance, depending on genes distributed in the different chromosomal types, explains the selection for heterotic combinations of chromosome orders in the lines selected for long wings, and for homozygosity in the selection for short wings, leading to greater response in the second case.

Prevosti (1966b) found a positive regression of the degree of structural heterozygosity on size in wild males from the site where the flies used to start the B selection lines were trapped. This suggests that the heterotic effect of the chromosomal types has not developed solely as a consequence of artificial selection, but also plays a role in natural populations.

Another point is that at least some structural orders of *D. subobscura* seem to have specific properties in relation to the genotype which controls size. The complex order usually fixed in the S lines must carry alleles which favour small size and this agrees with the high frequency of these orders in the southern populations, where the size of the flies is smaller. So, to some extent, it seems that when selecting for small size we are also selecting populations with some of the characteristics of southern populations. However, selection for large size does not lead to the chromosomal structure typical of northern populations, whose flies are of large size and in which there is a tendency to homozygosity for the standard orders (Knight, 1961; Sperlich, 1964). Instead, in the lines selected for long wings, there is a selection for standard orders but in heterozygous combination with the same chromosomal types fixed in the S lines. It is also significant that Robertson (1955) reported that several lines of *D. melanogaster*, selected for short thorax length became homozygous while parallel lines selected in the opposite direction remained heterozygous. It is curious that the combinations which are responsible for maximal heterosis are heterozygous for gene orders derived from the extremes of the geographical distribution. Perhaps this is only a statistical result related to the length of the inverted segments. The longer the inversion the greater the number of loci occupied by different alleles in each member of the inverted segments, which may result in a greater probability of heterosis due to directional dominance or overdominance. In any case it seems hazardous to draw general conclusions from the experiments at this stage.

Specific combinations of structural chromosome types have been associated with differences in body weight in the Australian grasshopper *M. scurra* by White & Andrew (1960, 1962) and White, Lewontin & Andrew (1963). In this species the geographical variation of body weight is very irregular and no correlation was found between the mean body weight and the frequencies of the chromosomal types in wild populations. The contrary is true of *D. subobscura*, where latitudinal clines in size (Prevosti, 1954, 1955*a*, *b*) parallel latitudinal clines in the frequencies of the

chromosomal types. So, in this case, it seems plausible to suggest that the origin of the chromosomal arrangements in different geographical areas and their adaptive value are interrelated.

As regards the heterotic effect of some combinations of the chromosomal types, the above-mentioned authors working with *M. scurra* only found heterosis in one colony, in which the greatest weight was found in individuals heterozygous for two pairs of chromosomes. Hence we have to be cautious in interpreting the heterosis found in the populations analysed here as being generally true for the chromosomal polymorphism of *D. subobscura*.

In another trait, rate of development, and another species of *Drosophila* (*D. persimilis*), Spiess & Spiess (1964, 1966) found selection for the trait to be effective in changing the frequencies of two allelic third-chromosome arrangements: selection for fast development always increased the frequency of the same arrangement and conversely, selection for slow development increased the frequency of the other arrangement. The heterokaryotype (Spiess, 1958) for these orders is intermediate between both homokaryotypes. So, considering these results together with those of *M. scurra* and *D. subobscura*, it seems to be the rule that the 'super-genes' created by inversion polymorphism of the chromosomes, differ in genes which control traits related to fitness. And these differences are not haphazard, but specific chromosomal orders have specific properties in relation to these traits. However, only in some cases do we find heterosis in heterozygous combinations of chromosomal arrangements.

In the major components of fitness the situation could be different. Spiess (1958), using the same chromosomal types as for rate of development, found that heterokaryotypes are superior in fecundity and viability to the corresponding homokaryotypes. Also, again using the same chromosomal orders, Spiess & Langer (1964) found differences in mating speed in carriers of each of these orders, but with some indication of heterosis in the heterokaryotypes.

SUMMARY

1. Selection for long or short wings was carried out in three pairs of lines of which two were started from the same basic population. At the end of the selection experiment the frequencies of the chromosomal arrangements were determined in each line and compared with the corresponding original frequencies to see if the chromosomal polymorphism of *Drosophila subobscura* is related to the genetic variation of size in a regular way.

2. The three pairs of lines show an asymmetrical response to selection. Selection for long wings is less effective in changing the mean of the population than selection for short wings.

3. Heritability is lower in the lines selected for long wings, especially in the later generations of selection.

4. Viability shows a very small decrease during selection in most selected lines.

5. In no case does the coefficient of variability show statistically significant changes, but there is a general tendency for it to decrease.

6. Selection for long wings favours combinations heterozygous for the standard chromosome orders and specific complex inversion orders. Selection for short wings generally fixes in homozygous combination specific complex inversion orders.

7. The heterozygous combinations of the standard chromosomal orders, which are most frequent in northern populations, when combined with the complex inversion orders which are most frequent in southern populations, have a heterotic effect on size.

8. The complex inversion orders usually fixed in homozygous combinations in the lines selected for short wings are those most frequent in southern populations which have a smaller mean size than northern populations.

9. The blocks of genes integrated in 'supergenes' in the inverted segments of the chromosomes of *D. subobscura* differ in genetic composition with respect to the control of wing length.

The author wishes to express his sincere thanks to Dr F. W. Robertson, who assisted him with the preparation and criticism of the manuscript, and also to Miss Maria Diaz who helped in the measurement of the flies in the B₁ and the B₂ lines.

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