Changing the relative size of the body parts of *Drosophila* by selection

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1. INTRODUCTION

The relative size of the organs and body parts of animals, in relation to general size and stage of development, has been recorded in many studies of allometry, but there appears to be little information about genetic variation in relative size at corresponding stages or the same adult size. Carson & Stalker (1947, 1949) have reported variation in shape among geographical races of *Drosophila robusta* and also seasonal variation by successive sampling in the same locality. Sokal (1959) scored a number of strains of *D. melanogaster* for various dimensions and found evidence of differences in proportion, although the differences between strains tended to fluctuate in successive generations for rather obscure, possibly environmental, reasons. With respect to vertebrates Clark (1941) has reported differences in the relative size of skeletal parts in *Peromyscus* while, more recently, Cock (in press) has demonstrated genetic differences in the skeletal conformation of the domestic fowl. There are, of course, various reports of differences between breeds of farm animals but there is little point in referring to them here. Although the origin and stability of the relative size of body parts can be treated in general terms, the actual differences in development between the skeleton of the vertebrate and the exoskeleton of the insect are so great that detailed comparisons are unprofitable.

Robertson & Reeve (1952) reported changes in the wing/thorax ratio of *Drosophila melanogaster* among lines selected for either long or short wings or larger or smaller thorax. Although selection for either wing or thorax length proved an effective way of altering body-size, there was also relatively greater change in the particular dimension used for selection. Reeve (1950) estimated, from these data, a genetic correlation of about 0·7 between wing and thorax length, noted a discrepancy between estimates derived from the comparisons between selected lines and the higher values generally found in progeny tests in the unselected population, and emphasized the need for more systematic study of the genetic correlation between the sizes of body parts. It appears to be tacitly assumed in the literature that the relative size of body parts, among strictly comparable individuals of a given species, is more or less constant. Ratios of dimensions are often used as systematic criteria. It is of some interest, therefore, to see whether the relative size of body parts can be substantially altered by selection and, if so, to determine the general genetic behaviour of such differences.

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The present paper describes the results of selecting for high- and low-ratio of wing/thorax size in a population of *Drosophila melanogaster*. After ten generations of selection, the selected strains, the unselected population and various crosses between them were compared under different conditions of temperature and nutrition. Leg size was also recorded for some of these treatments to test for correlated changes in other dimensions.

2. MATERIAL AND METHODS

The Pacific population, which has been run for several years in a population cage, was used in these experiments. Selection was carried out by recording the wing/thorax ratio for ten pairs of flies from each of five replicated cultures. The extreme two pairs per culture were then combined to give ten pairs selected from fifty pairs. For the first five generations selection was based on an estimate of wing area to thorax length, using the product of wing length and breadth as an index of area. This was done to avoid possible selection for differences in wing shape. In later generations the simple ratio of wing to thorax length was used. There is no evidence that wing shape has been altered by selection in either direction.

At the end of the experiment, after ten generations of selection, a series of replicated cultures from the selected strains, the cage population and all possible crosses were set up under favourable conditions at 29°, 25° and 18° C., and also adverse conditions at 25° C. With the latter treatment larvae were crowded on a sparse diet and this led to a substantial reduction of body-size. For the two treatments at 25° C. one each of the three pairs of legs was mounted and the tibia length was measured with the aid of a micrometer eye-piece. Records of wing-size in this experiment were derived from planimeter records of an enlarged image of the wing; one wing per fly was mounted. Thirty to forty females, drawn from four to five replicated cultures, were scored for each category, unless otherwise stated.

For analysis of the effects of selection in these final comparisons all records of thorax length, wing area or length and tibia length have been transformed to natural logarithms. In the Tables which show differences between means, the calculated values have been multiplied by 10^2 and so they are roughly equivalent to percentage differences. Variances have been multiplied by 10^4. For the record of selection response in successive generations, the average ratio of wing to thorax length has been used. During selection, flies have been grown on the usual maize-meal molasses medium at 25° C.; methods of measuring live flies have been given elsewhere (Robertson & Reeve, 1952). For comparing the relation between wing or leg size and thorax length in different strains the regressions on thorax length have been used. Since this dimension is so highly correlated with body-weight it is hardly necessary to use the otherwise better method of computing differential growth ratios suggested by Haldane (1950).

3. RESULTS

(a) *The response to selection*

This is shown in Fig. 1. The top graph represents the deviation from unselected of the average ratio of wing to thorax length for females only. Unselected controls

were measured only from generation 3 onwards. There is some evidence of asymmetry since, at first, there was greater change in favour of lower ratio, but the differences are less apparent at a later stage of selection. The middle graph shows the
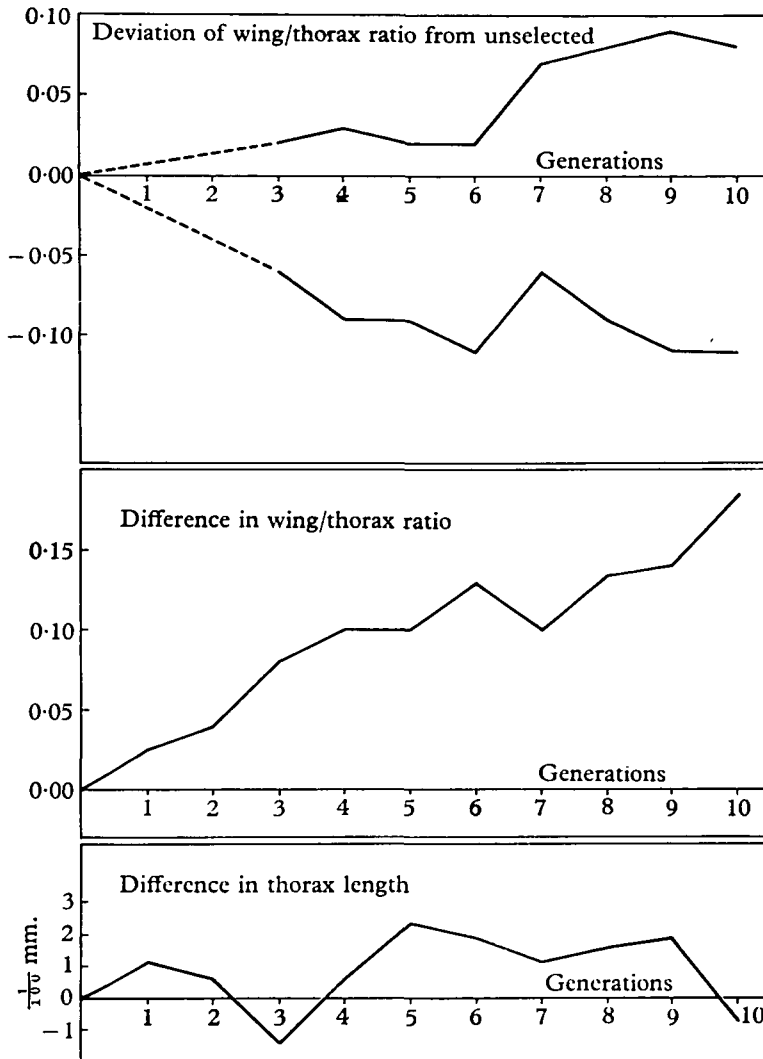

Fig. 1. The response to selection for relatively longer and smaller wings. Apparent minor discrepancies in the alternative records of selection response are due to the use of data from females only in the upper graph since unselected control females were measured from generation 3 onward. In the other graphs data from both sexes have been averaged.

differences between the lines for each generation in terms of the average of both sexes. The two lines moved steadily apart and, by the 10th generation, there was a substantial difference in relative wing size. There is no evidence that the response had ceased by the time the experiment was terminated.

The bottom graph shows what happened to thorax length during selection. The average difference between the lines, sexes averaged, is expressed in hundredths of a millimetre. Since the average thorax length of unselected males and females, grown under the same conditions, is about a millimetre, the differences are approximately equivalent to percentages. There is a tendency for the high-ratio line to have a slightly larger thorax but this may well be an uncorrelated effect of sampling or linkage. By comparing the middle and lower graphs we can infer with certainty that thorax size has been virtually unaffected by the changes in relative wing size.

Heritability has been estimated from the regression of the differences between the selected lines, sexes averaged, on the cumulated selection differential required to produce these differences. The regression has been estimated on data from the first five generations of selection rather than all available generations, since the further selection proceeds the less applicable are such heritability estimates to the variation in the unselected population. The regression estimate works out at 0.56 ± 0.08 so there is no doubt that genetic variation in relative wing size is both appreciable and highly heritable in the Pacific population.

(b) Comparisons between lines—wing size

We have now to consider how much change in wing area has been caused by selection after making due allowance for possible differences in general body-size. Within any population of *Drosophila* there is a high phenotypic correlation between wing and thorax size due to the combined effects of both genetic and environmental variation. Genetic correlations of 0.8 have been recorded (Reeve & Robertson, 1953) and chromosome substitutions between selected strains have further demonstrated

Table 1. *Differences in log (thorax length) between strains—deviations from unselected*

	Optimum			Crowded
Genotype	29° C.	25° C.	18° C.	25%
H	-3	-4**	-3	1
L	-3	-2*	-3	1
$H \times L$	—	-1	—	—
$U \times H$	—	-1	—	—
$U \times L$	—	-1	—	—

U, H and L refer to the unselected populations and the high- and low-ratio lines respectively. Single and double asterisks indicate differences significant at the 0.05 and 0.01 level of probability. The log values have been multiplied by 100 and rounded off to the nearest unit.

the close association between these two dimensions (Robertson & Reeve, 1953). In the present experiment, since selection was for relative wing size, we neither anticipate nor find that selection in opposite directions alters thorax length. But in the comparisons between strains and crosses at the end of the experiment, it turns out that the thorax length of both selected lines is slightly but significantly smaller than that of the unselected flies. The differences for various treatments are shown in Table 1. Such minor differences probably represent some inbreeding decline in

general body-size due to higher levels of homozygosity which result from the combined effects of small population size and selection. This is consistent with the fact that the F_1 between the high- and low-ratio lines does not differ significantly from the unselected.

Such differences, although comparatively small, have to be allowed for if we are to arrive at the most accurate estimate of the differences in wing size at the same average thorax length. In applying the usual regression analysis for wing area and thorax length, we must first look for possible differences between the lines and the unselected population in the wing/thorax regression. Table 2 shows the regression coefficients for the within-culture variance for the different series and treatments, together with tests of heterogeneity. For the unselected and both the high- and low-ratio lines, the estimated differences in slope between the treatments are on the

Table 2. *Regressions of wing area on thorax lengths (logs) based on the pooled within-culture variances*

	Strains		
Treatments	U	H	L
Optimum:			
29° C.	$1·33 \pm 0·31$	$2·02 \pm 0·27$	$1·03 \pm 0·64$
25° C.	$1·02 \pm 0·35$	$1·35 \pm 0·21$	$0·45 \pm 0·29$
18° C.	$1·69 \pm 0·23$	$0·96 \pm 0·10$	$0·82 \pm 0·55$
Crowded:			
25° C.	$1·68 \pm 0·44$	$1·79 \pm 0·29$	$1·12 \pm 0·23$
Differences in slope	$P > 0·05$	$P > 0·05$	$P > 0·05$
Pooled regressions	$1·38 \pm 0·12$	$1·49 \pm 0·15$	$0·85 \pm 0·28$

border line of statistical significance, although there are substantial differences in mean. The within-culture effects have been pooled over all treatments. The regression of log (wing area) on log (thorax length) for the high-ratio line, unselected population and the low-ratio line work out at respectively $1·49 \pm 0·15$, $1·38 \pm 0·12$ and $0·85 \pm 0·28$. Comparing the residual variance from parallel lines fitted to the three series with the residual variance from separate lines shows that these suggestive differences fall just inside the 0·05 level of significance. However, the trends among the separate regression coefficients suggest that the observed differences reflect real rather than sampling differences. If so, it means that selection for high- and low-wing ratio has altered the allometric relations between wing and thorax length for the genetic and environmental differences between individuals within cultures, so that a given change in thorax length is accompanied by changes in wing size which are proportionally greater for the high-wing than the low-ratio line.

These separate estimates for the three series have been used to adjust the observed mean wing lengths in each set of comparisons to correspond to the grand average thorax length for each treatment. As noted above, the differences in thorax length are small and so this procedure makes very little difference in practice. The values for wing size for the different treatments are set out in Table 3 as deviations from

unselected. At 25° C., under favourable conditions, wing area in the high-ratio line is some 13% bigger while in the low-ratio line it is about 17% smaller, a total difference of about 30% for the same thorax length. For the high-ratio line, the 12–13% difference is maintained at all temperatures under favourable conditions, but is reduced to 8%, a statistically significant difference, when the larval diet is in-

Table 3. *Differences in wing area between selected lines*

	Deviations from unselected—logs $\times 10^2$			
	Optimum			Crowded
Genotype	29° C.	25° C.	18° C.	25° C.
H	12	13	12	8
L	−16	−17	−12	−15
Total difference	28	30	24	23

adequate. In the low-ratio line, the same deviation holds for all treatments except culture at 18° C., for which wing area is only about 12% smaller—also a statistically significant difference. At this temperature both high- and low-ratio lines deviate from the controls to the same extent. The reduction in relative wing size in the high-ratio line in crowded cultures could be interpreted in terms of priorities for nutrients but there is no obvious reason why lower temperature should alter the ratio in the other line.

(c) *Changes in leg dimensions*

As noted above, tibia length was recorded for one member of each of the pairs of legs of flies grown under both favourable and unfavourable conditions at 25° C. Like wing length, tibia length is also highly correlated with thorax size and for the same reasons; so the same treatment is called for. The regression analysis of the within-culture variance and covariance failed to detect any significant difference in regres-

Table 4. *Regression of tibia length on thorax length*

	Genotype		
Treatment	U	H	L
Optimum	0.72 ± 0.18	0.66 ± 0.12	0.37 ± 0.11
Crowded	0.63 ± 0.03	0.53 ± 0.14	0.75 ± 0.09
Heterogeneity in slope	$P > 0.05$	$P > 0.05$	$0.05 > P > 0.01$
Pooled regressions	0.66	0.58	0.59

sion slope between the three legs for either treatment and so the within-culture effects have been pooled to provide the regression estimates which are shown in Table 4. Neither for the unselected population nor for the high-ratio line is there any significant difference in slopes between treatments. But in the low-ratio line the regression works out at 0·37 for optimal conditions compared with 0·75 for sub-optimal—a difference which is just significant at the 0·05 level. The estimate for the

pooled within-culture effects, pooled over both treatments, is closely similar to the corresponding values for the unselected population and the high-ratio line. Perhaps too much importance should not be attached to the differences in slope between treatments in the low-ratio line. If so we may be justified in pooling all the within-culture variance and covariance for the three series and the two treatments. This yields a regression of log (tibia length) on log (thorax length) of 0·60, and this value has been used to adjust the observed means of log (tibia length).

Table 5. *Correlated changes in tibia length*

		Deviation from unselected—logs $\times 10^2$			
Treatment	Genotype	Leg 1	Leg 2	Leg 3	Average
Optimum	H	1·3 *	1·0	4·7 **	2·3
	L	− 5·5 **	− 2·7 **	− 3·4 **	− 3·9
Crowded	H	1·5 **	3·0 **	1·9 **	2·1
	L	− 3·5 **	− 1·8 **	− 2·2 **	− 2·5

Single and double asterisks indicate significance at the 0·05 and 0·01 levels of probability.

The values are expressed as deviations from unselected in Table 5. They reveal the unequivocal result that selection for change in relative wing size has led to correlated changes in relative leg size. The more effective selection for low-wing than high-wing ratio is also paralleled in the greater relative reduction in tibia length. Thus a few generations of mass selection have sufficed to produce major differences in body proportions.

(d) *Cell size and number*

It has been shown elsewhere (Robertson, 1960) that changes in body-size which are due to different kinds of genetic or environmental change are often associated with characteristic difference in the cellular make-up of the wing. It is of interest, therefore, to discover how the present differences in wing size have been produced.

Table 6. *Comparisons of wing cell size*

	Deviations from unselected—logs $\times 10^2$	
Genotype	Wing area	Cell area
High ratio	13	1·6
Low ratio	− 17	− 1·6
Difference between lines	$P < 0·001$	$P > 0·05$

Wing cell size is estimated from the density of bristles in a central region of the upper wing surface. Each bristle marks a cell and so the average surface area occupied by a cell can be derived from counts on a greatly magnified image. The comparisons in terms of log (cell area) and log (wing area) are shown in Table 6. In spite of some 30% difference in wing area, the average cell area does not differ significantly between the

two selected lines. It may be inferred therefore that the relatively larger or smaller wing size is due to corresponding increase or decrease in cell number. This genetic difference may be contrasted with the changes in wing/thorax ratio which can be produced by growing flies at different temperatures. Lower temperature leads to relative increase of wing area and this is effected by corresponding increase in cell area (Alpatov, 1930; Robertson, 1960), so similar changes in ratio by either environmental or genetic means are effected by quite distinct differences in development. The apparent independence between cell size and relative wing size lends added significance to changes of cell size which are correlated with thorax length and which reflect variation in general body-size.

(e) *Genetic behaviour*

As part of the final comparisons, under optimal conditions, between the unselected population and the two lines at 25° C., all three series were intercrossed as well and wing area was recorded in the usual way. Two generations later a further experiment was carried out to allow comparisons between the parent strains, the F_1 of the cross between the unselected population and either the high- or the low-ratio line and also the two alternative backcrosses of each F_1 to each of the appropriate parent strains. The test was so arranged that cultures of all these types were set up at the same time. There is no evidence that a generation or so of relaxed selection leads to any appreciable alteration of the characteristic wing/thorax ratio. In this test wing length was scored. Measurements of wing length and breadth in samples of flies of each selection line showed that wing shape had not been significantly altered and so wing length is entirely adequate as an index of wing size.

Table 7. *The effects of intercrossing strains—log (wing area) adjusted to standard thorax length* $\times 10^2$

Cross	F_1–Mid-parent	Unselected–F_1
$U \times H$	0·1	− 6·4 **
$U \times L$	4·2 *	4·2 *
$H \times L$	11·0 **	− 8·9 **

* and ** indicate significance at the 0·05 and 0·01 levels of significance.

The results of the first of these two tests are shown in Table 7 as deviations of the F_1 from the mid-parent value. For the cross between unselected population and the high-ratio line the F_1 is precisely intermediate but in crosses to the low-ratio line the F_1 value significantly exceeds the mid-parent value—by some 11% in the cross between high- and low-ratio lines.

This comparatively recessive behaviour of differences favouring relatively smaller wing size was further revealed in the more extensive experiment. In this case the departure from additivity can be expressed more quantitatively by applying the usual type of least squares analysis to the observed mean size of parents, F_1 and each pair of backcrosses to estimate the value expected for the various series. The mean

square of the deviation between the observed and expected values is tested against the error variance of a mean, which, in turn, is derived from estimates of within and between-culture components of variance. Table 8 shows that for the un-

Table 8. *Test of departure from additive behaviour in crosses and backcrosses*

Cross	$H \times U$	$L \times U$
Mean square deviations between observed and expected values	16·7	34·4
Degrees of freedom	3	3
Error mean square	6·5	6·5
Degrees of freedom	451	451
F	2·56	5·22
	$P > 0.05$	$0.01 > P > 0.001$

H, L and U refer to the high- and low-ratio lines and the unselected population.

selected × high-ratio series the deviations between the observed values and those expected on the least squares analysis are within the limits of sampling and so the genetic behaviour is additive, within the limits of such a test, whereas in the other series there is a highly significant departure from additive combination. There is therefore a clear difference in genetic behaviour according to whether the changes have led to relatively larger or relatively smaller wing size.

4. DISCUSSION

This experiment suggests that the relative size of the appendages of the insect exoskeleton can be readily altered by selection. There is no reason to doubt that further selection and/or more efficient selection procedures could lead to greater changes in the wing/thorax ratio than those reported here. In the unselected population, although variation in general body size accounts for the high correlation between thorax and either wing or leg size, there evidently remains an appreciable fraction of the variance of the appendages which is independent of changes in thorax length. If the total mass of the exoskeleton, including legs and wings, tended to remain constant we should anticipate evidence of a negative correlation between thorax size and the size of the appendages, but there is no trace of this since a 30% difference in wing size was accompanied by hardly any difference in thorax length between the selected lines. Differences in mass can be effected either by changes which affect the growth of all parts equally or by alterations in the relative growth of parts. Since body-weight was not recorded in these experiments this aspect can hardly be pursued further.

The correlated change on the part of wing and leg size means that the growth and differentiation of their imaginal discs are under common genetic control. According to Bodenstein (1950) the imaginal hypodermis is derived from the anterior cells of

the imaginal discs which proliferate to replace completely the larval hypoderm about 8 hours after puparium formation. Selection for change in the wing/thorax ratio could conceivably alter the growth rate of the imaginal discs during the larval period but the constancy of thorax size would appear to require regulation in the proliferation of cells from the imaginal disc destined to form thoracic hypoderm. On the other hand, the characteristic differences may be confined to alteration of the relative growth rate of the presumptive thorax and wing or leg cells during the early pupal period and this would not conflict with the evidence that selection in opposite directions has led to corresponding changes in the allometric relations between wing and thorax length. It is perhaps not surprising that tissues of such similar embryological origin and developmental history should react in the same way. But an intrinsic tendency to do so is likely to be reinforced by the precise synchronization of growth rates and differentiation which is required in the process of replacing larval by imaginal hypoderm. Such developmental relations between the different appendages is likely to be highly stable and homeostatic, although the relative size of the appendages, as a group, may be free to vary within wide limits.

A systematic study of the effects of selecting for different kinds of proportional change in body parts would provide valuable evidence on the relative constancy or lability of the growth patterns which determine morphology. Indeed certain questions can be answered only in this way. Selection is a useful tool which remains largely unexploited by students of physiology and development. Planned changes in growth and form can provide a wide range of differences for comparison and analysis.

Although it is easy to make substantial changes in the relative size of the wing, it is also true that the wing/thorax ratio remains comparatively constant in different races of the species (Robertson, 1960). At first sight, relative wing size would appear to belong to the category of characters which vary about an intermediate optimum. It is reasonable to suppose that there is an optimum wing size, relative to body-weight, for maximum efficiency of flight under the conditions to which the species is adapted. But wing size may play a role in other activities as well. Thus Ewing (in press) has shown that there is an inverse relation between wing area and the time to successful completion of courtship by the males and that this relationship also holds for the present strains which differ in wing size. Hence wing size may be held to its characteristic relative value by a combination of different kinds of selection pressures.

But the inference that relative wing size varies about an intermediate optimum needs amendment since there is circumstantial evidence to the contrary. From general experience of the inheritance of different kinds of character, variation about an intermediate optimum is generally associated with additive genetic behaviour, whereas highly non-additive effects have been encountered in the inheritance of relative wing size. The crosses between strains showed that relatively smaller wing size behaves as if the genetic differences were more or less recessive in crosses to either the unselected population or the high-ratio line, whereas in crosses between the latter and the unselected population there is no apparent departure from addi-

tivity. This suggests that dominance, and probably also complementary interaction between loci, together contribute to the stability of the normal wing/thorax ratio, by lowering the probability of occurrence, in a genetically variable population, of individuals with relatively smaller wing size, which is thus held to an upper rather than an intermediate level. The probability of additive behaviour of allelic differences is thus conditional on the genetic background, especially on the direction and extent of the deviation from the mean. Progressive reduction in wing size will increasingly depend on different kinds of growth limitation which do not occur among individuals of either the unselected population or those selected for larger relative wing size, in which the level of additivity is therefore highest.

The situation recalls precisely the situation with respect to general body size in which recessive and hypostatic behaviour with extensive non-allelic interaction is progressively established during selection for smaller size (Robertson, 1961). The additivity in crosses between the unselected and the high-ratio line parallels the relatively more additive behaviour in the effects of interchanging chromosomes between large and unselected lines (Robertson & Reeve, 1953). There is little doubt, therefore, that selection for relatively smaller wing size will progressively establish a genetic situation in which genes which tend to restrict growth, in that particular genetic complex, behave as recessive and/or hypostatic. This will favour fixation and continued response until genetic variation is exhausted. This is relevant to the observation in early experiments (Robertson & Reeve, 1952) that although selection for long or short wings led to larger or smaller body-size, the wing/thorax ratio was little changed in the former but was reduced in the latter, in which reduction in general body-size and relative wing size will both show similar genetic behaviour. Indeed, in one instance, the disproportionate reduction in wing size was traced to recessive sex-linked effects.

SUMMARY

1. Mass selection for both high- and low-ratio of wing to thorax length has been carried out on a population of *Drosophila melanogaster*. The response to selection was immediate and sustained. When the experiment was stopped after ten generations, the wing area in the two selected lines differed by about 30%. The heritability estimate worked out at 0.56 ± 0.08.

2. Thorax length remained comparatively unchanged during selection nor was there any change in wing shape. There was some evidence of assymetry of response since there was a relatively greater change in favour of smaller rather than larger size.

3. The tibia length of all pairs of legs showed correlated changes so that the lines with larger or smaller wing sizes had also larger and smaller legs.

4. The normal allometric relation between wing and thorax length, associated with variation in body-size, apparently also changed, so that for a given change in thorax length there was a greater or smaller proportional change in wing size in the high- or low-ratio lines.

5. The changes in relative wing size are due to changes in cell number.

6. It is suggested that the genetic changes due to selection act in the early pupal period when the imaginal discs are undergoing differentiation and proliferation to form imaginal hypoderm and appendages.

7. Tests of genetic behaviour failed to show any departure from additivity in crosses which involved the unselected population and the high-ratio line. But highly significant departures existed in the cross to the low-ratio line. Relatively smaller wing size behaves as largely recessive. Stability of the normal wing/thorax ratio involves dominance and probably also epistasis. The genetic properties of the relative size of the appendage are apparently similar to those which characterize body-size as a whole.

8. It is suggested that selection provides a valuable tool for studying the constancy or lability of the growth patterns which determine morphology.

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