VARIATION FOR METRICAL CHARACTERS IN *DROSOPHILA* POPULATIONS

III. THE NATURE OF SELECTION

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1. Introduction

An earlier paper (Kearsey and Barnes, 1970) reported the results of experiments investigating the relationship between sternopleural chaeta number and fitness in a cage population of *Drosophila melanogaster*. The population studied was derived from a cross between two lines, produced by selection for high and for low number of chaetae from our " Texas " population (Barnes and Kearsey, 1970), and subsequently allowed to evolve under cage conditions.

It was shown that the phenotypic variance of adults captured in the cage, the survivors of intense larval competition, was approximately one-quarter that of their contemporaries raised at very low density. Furthermore, this decrease in phenotypic variance was shown to be due, almost exclusively, to a decrease in genetic variance. That is, there has been selective elimination of certain genotypes at the pre-adult stage. This selective elimination was related to chaeta number. It was then possible to estimate the relative fitness of different phenotypes by comparing their relative frequencies at the two larval densities.

By this means fitness was shown to be greatest for phenotypes with a value close to that of the F_1 between the parental selection lines and to decline markedly with deviations in both directions from this optimum, reaching a fitness of zero within the phenotypic range. Such a reduced fitness of extreme phenotypes might be due to association between genes controlling chaeta number and subvital genes fixed during the establishment of the parental selection lines. That is, the selection lines may contain a number of recessive subvital genes linked to genes for sternopleural chaeta number and this association might still be present at the time of the experiment. Extreme phenotypes will tend to be homozygous for such subvitals, whereas intermediate phenotypes will be heterozygous and hence have higher fitness. However, the detailed relationship between phenotype and fitness was not consistent with the relationship generally found in such cases. Although linked subvitals might in part be the cause, it was argued that the results are more compatible with stabilising selection.

The relationship between chaeta number and fecundity, on the other hand, was entirely consistent with a system of dispersed subvital genes. However, females extreme for chaeta number do not reach adulthood under cage conditions and as a consequence the variation in fecundity had no impact on fitness. The major component of fitness in this case appears to be egg to adult survival.

The experiments to be described here were designed to test the validity of the two principal conclusions drawn previously. Firstly, that selection is concerned directly with genes controlling chaeta number as opposed to linked deleterious genes (Experiment 1). Secondly, given that the first conclusion is correct, that selection is based on metric deviation rather than heterozygote advantage at the loci controlling chaeta number (Experiment 2). Selection on the basis of metric deviation implies that the fitness of an individual is solely a function of its phenotypic deviation from an intermediate optimum and does not depend directly on the number of loci at which it is heterozygous.

2. Experiment 1

If the decreased fitness of extreme phenotypes is due to linked subvital genes, then the relationship between chaeta number and fitness found in the derived population should not apply in the base population. The first experiment was designed to assess selection in the base population.

The " Texas " population has been maintained for 6 years in this laboratory and the mean and variance have not changed noticeably in that time. Given the hypothesis that the genes controlling chaetae are neutral, such genes will be in linkage equilibrium with respect to any subvital genes since the population is large (about 3500). Hence the hypothesis is disproved if a reduction in the *genetic* variance for chaeta number can be demonstrated, as a result of crowding. In the previous experiment (Kearsey and Barnes, *loc. cit.*) the decline in *phenotypic* variance was so great as to be explicable only in terms of a reduction in *genetic* variance. The *phenotypic* variance of " Texas ", on the other hand, is small even at low larval densities and declines little on crowding. This leads to difficulties in interpretation. While it is easy to demonstrate a significant decline in phenotypic variance (if sufficient flies are scored) the difference, being small, could be due to one, or a combination, of the following factors operating at high density:

1. A reduction in the effect of individual gene substitutions.
2. A reduction of the environmental variance.
3. The selective elimination of extreme phenotypes.

The first two points involve genotype environment interaction while (3) alone involves selection. The regression techniques used previously are insufficiently sensitive to discriminate between these possibilities in the present case. However, the effects of genotype environment interaction may be excluded by progeny testing phenotypes in the same environment. This was achieved by crossing a random sample of the males surviving at both high and low density to virgin females of an inbred tester line. Their genetic variance for chaeta number was then assessed from the performance of their progeny raised under uniform environmental conditions. Selection at high density will result in a reduced variance between families of high-density males compared to that of their contemporaries raised at low density. Furthermore, fitnesses can be estimated from the relative frequencies of different family means derived from parents at high and low densities. The advantage of this approach is that it excludes genotype environment interaction affecting the variances and also obviates the need to correct the

phenotypes of flies raised at high density for the direct environmental depression of chaeta number produced by food deprivation.

(a) *Method*

The wild population used in these studies, " Texas ", originated from 30 inseminated females caught at Austin in Texas in October 1965, and subsequently maintained in a population cage (Barnes and Kearsey, 1970). One thousand eggs were collected from the cage population and incubated in tubes containing standard oatmeal medium at a density of 50 eggs per tube. After eclosion, a random sample of 250 males was collected and scored (low-density sample), and at the same time a sample of 250 males was collected from the cage and scored (high-density sample). Two days later, all the males surviving in the two samples were mated individually to four virgin females from the inbred line Oregon, and the progeny raised in tubes. All the families were incubated in a single randomised block at 25° C. Five female progeny were scored from all successful matings 11 days later.

The size of the experiment was determined from a pilot study involving only 30 males from each density carried out by our colleague Mr A. Birley.

(b) *Results and discussion*

The mean and variance of the male parents used in the progeny tests and of their female offspring are shown in table 1. The mean chaeta number

TABLE 1

Summary of data from progeny tests on males from low- and from high-density conditions. Five female progeny scored from crosses between sample males and Oregon females

	Density	
	High	Low
Number of ♂♂ sampled	133	187
Mean of ♂♂ sampled	15·8045	16·9393
Variance of ♂♂ sampled	2·6736	3·2693
Mean of ♀♀ offspring	19·5895	19·5359
Variance of offspring family means	1·1602	1·6093
Average variance within families	2·7975	2·7390

of flies raised at high densities is significantly less ($P < 0{\cdot}001$) than for flies raised at low density, as was found previously (Kearsey and Barnes, *loc cit.*). The variance, although reduced at the high density, is not significantly less than the low-density variance ($0{\cdot}10 > P > 0{\cdot}05$).

Turning now to the offspring data, we find that the means do not differ significantly ($0{\cdot}3 > P > 0{\cdot}2$). However, the variance of family means of progeny obtained from male parents raised at high density is very significantly reduced ($P \simeq 0{\cdot}025$). A conventional one-tail variance ratio test was used here as, from our previous evidence, we expect the variance to be greatest at low density. Furthermore, this decrease in the variation *between* families must indicate a reduction in the genetic variance at high density as the *within* family variances at the two densities are homogeneous.

This reduction of the genetic variance can be shown more clearly by the regression analyses given in table 2. The variation between family means has been partitioned into the following items.

1. The variation due to the regression of progeny onto male parent.
2. The variation resulting from departures from linearity of this regression.
3. The variation between families derived from male parents of the same phenotype.

The remainder mean square (2) is not significant for either treatment. Thus there is no evidence of non-additive genetic variation. Items 2 and 3 have therefore been combined to give the pooled residual items of table 2. Furthermore, there is no significant difference between the residual items from high and low density. The regression items are highly significant at

TABLE 2

Regression analysis (based on family means)

	Density					
	High			Low		
Item	d.f.	M.S.	P	d.f.	M.S.	P
1. Regression on ♂ parent	1	14·0938	<0·0001	1	77·5796	<0·0001
2. Remainder	7	1·3380	>0·20	8	1·1645	N.S.
3. Between families within ♂ phenotypes	124	1·0458	<0·001	177	1·2002	<0·001
Pooled residual	131	1·0615	—	185	1·1986	—
Within families	532	0·5595	—	748	0·5478	—

Regression of family mean on to ♂ parent $\hat{b}_H = 0{\cdot}19984 \pm 0{\cdot}0548$ $\hat{b}_L = 0{\cdot}35718 \pm 0{\cdot}0444$

both densities, indicating the presence of additive genetic variation. The estimated slopes of these regressions $\hat{b}_H$ and $\hat{b}_L$ are given in table 2. The difference between the slopes is highly significant ($P \simeq 0{\cdot}025$), $\hat{b}_H$ being approximately half $\hat{b}_L$.

Thus the regression analysis has clearly shown that the decline in genetic variance amongst the males raised in the cage can be explained solely by a reduction in the additive genetic variance. The regression slopes, $\hat{b}_H$ and $\hat{b}_L$, are equivalent to half the narrow heritability, h^2, of the two male samples. In the absence of non-additive variance we can estimate the magnitude of the additive genetic variance, V_A, and the environmental variance, V_E. These estimates are as follows.

	$\hat{h}^2$	$\hat{V}_A$	$\hat{V}_E$	$\hat{V}_P$
Low	0·7144	2·34	0·93	3·2693
High	0·3997	1·07	1·60	2·6736

It appears, therefore, that not only is there selective elimination of certain genotypes at high density, as shown by the reduced additive genetic variance, but also the environmental variance is increased.

Let us now turn to the nature of this selection. The average breeding value of the two samples of males do not differ, *i.e.* the progeny means are not significantly different, but the genetic variance is reduced amongst those individuals raised in the cage. This must indicate selection against extremes. Further information on the type of selection may be obtained if we can

ascribe a relative fitness to each phenotype. Previously fitnesses were obtained by comparing the frequencies of phenotypes produced at high

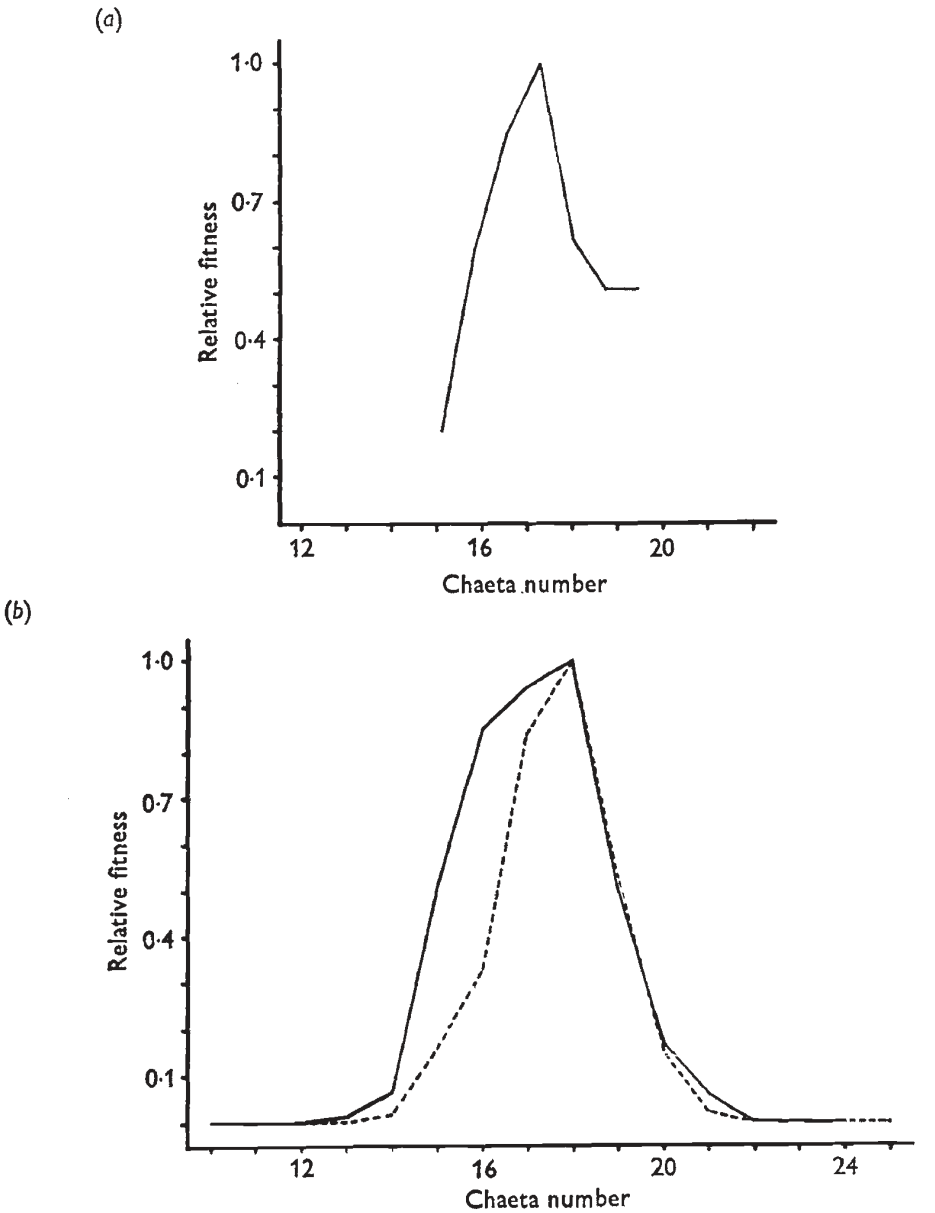

FIG. 1.—The relationship between chaeta number and relative fitness for (*a*) males sampled from the " Texas " population (Expt. 1) and (*b*) homozygous males (solid line) and females derived from the " Texas " population (Expt. 2).

density with the frequencies obtained at low density (Kearsey and Barnes, 1970). In the present case we have to compare progeny means, and a difficulty is that these means differ by multiples of 0·2 bristles; consequently

there are relatively few observations for each value. A poor estimate of fitness would be obtained therefore if these frequencies were used directly. This may be overcome by combining the progeny means in groups of five such that the mean of each set is an integer. Thus, the frequencies of progeny with a mean of 15·6, 15·8, 16·0, 16·2 and 16·4 were combined to give a single frequency for an overall progeny mean of 16. A comparison of the frequencies for each integer value obtained at the two densities then gives us a measure of relative fitness. These fitnesses may be rescaled such that the optimum has a value of unity. The fitnesses obtained in this way relate to the *progeny* phenotype. However, for our present purposes it is more useful to express the fitness in terms of the phenotypes of the males originally sampled from the " Texas " population. This conversion is achieved from the regression of the male parents on to the family means. These predicted values together with their fitness are shown in fig. 1(a).

It can be seen that males with a phenotype of 17·3 have optimum fitness, and fitness declines with phenotypic deviations from this optimum. The fitness relationships are consistent with those obtained previously in the derived population, apart from the lower optimum phenotype of 17·3 as compared to that of 20 for the derivative.

3. Experiment 2

The second experiment was designed to test the validity of the conclusion that selection is for metric deviation as opposed to heterozygote advantage at the loci controlling chaeta number. The intention was to investigate a population which consisted of a heterogeneous collection of homozygotes taken from inbred lines which had been derived from the " Texas " population by sib-mating. The optimum phenotype in the base population when these inbred lines were established was 18 chaetae, and we would expect a similar optimum to be appropriate to the population of homozygotes if we are concerned with a metric deviation model of stabilising selection. With such a homozygous population, heterozygote advantage cannot, of course, be invoked to explain any relationship between phenotype and fitness.

(a) *Method*

A sample of 22 inbred lines were derived by sib-mating the progeny of single-pair matings among individuals from the " Texas " population for 42 generations. From this set of lines, four were taken (lines 10, 20, 25, 28) for use in the present experiment; these lines were chosen in such a way that a population produced by mixing them in equal proportions would contain at least some individuals of each phenotypic class in the range 12-22 sternopleural chaetae, with most classes containing members from more than one line.

In order to test lines 10, 20, 25 and 28 for the presence of residual heterozygosity at the loci controlling chaeta number, individuals within each line were positively assortatively mated for chaeta number. Two replicate single-pair matings were used throughout, and 10 progeny of each sex were scored from each cross. The extent of genetic variation can be assessed from the regression of offspring on parent.

The technique used in the main experiment is a modification of that

employed by Kearsey and Barnes (1970). Essentially, two larval environments were used, one in which the larvae were raised at low density, the other in which larvae were raised at high density, under intensely competitive conditions. Two populations were constructed, by introducing 125 inseminated female adults from each of the four inbred lines into each of two population cages. The cage that was to provide the low-density larval environment contained 20 food-tubes with the standard oatmeal/yeast medium, and the high density cage 5 food-tubes. The 500 females in each cage were allowed to oviposit for 7 days, and were then removed from the cages. The experiment was carried out at $25 \pm 0{\cdot}5°$ C. The first progeny emerged from the low-density cage on the third day after the removal of their mothers.

A random sample of 500 flies of each sex from the total number that emerged over a 10-day period from the low-density cage was scored for

TABLE 3

Mean chaeta number of " Texas " inbred lines 10, 20, 25, 28

Line	♂♂	♀♀
10	$12{\cdot}80 \pm 0{\cdot}98974$	$14{\cdot}02 \pm 0{\cdot}87714$
20	$17{\cdot}12 \pm 1{\cdot}28793$	$17{\cdot}28 \pm 1{\cdot}27839$
25	$16{\cdot}72 \pm 1{\cdot}29426$	$16{\cdot}78 \pm 0{\cdot}95383$
28	$21{\cdot}50 \pm 1{\cdot}55511$	$21{\cdot}88 \pm 1{\cdot}42342$

chaeta number, as were all those emerging from the high-density cage over a similar period.

Males and virgin females, from both cages, were progeny-tested, by mating them individually to a common inbred tester line, Oregon. From each density, males and females with chaeta numbers 13-19 inclusive were used, and for each phenotypic class two replicate single-pair matings were set up. Their progeny were raised, at low density, in the usual 7·5 cm. $\times$ 2·5 cm. diameter food tubes, the experiment taking the form of a single randomised block. Ten progeny of each sex were scored, per mating, for chaeta number, and the regression of offspring on " Texas " inbred parent calculated. This resulted in eight simple regressions, *viz.* son on father, daughter on father, son on mother, and daughter on mother, for each density.

(b) *The amount of within-line heterozygosity*

The mean chaeta numbers of the four lines, based on samples of 50 individuals of each sex, are shown in table 3.

The regression analyses of offspring on parent carried out within each of the lines are shown in table 4; there were no significant differences between replicate crosses, and this item in the analysis has, in every case, been combined with the variation within crosses. In each line some detectable genetic variance remains, and appears, inconsistently, in the eight analyses. To obtain some idea of the magnitude of this residual variation, the genetic component of variance, σ^2_G, between families has been estimated in those cases which show significance of either the Regression or the Remainder M.S. These components of variance are as follows:

Line	Sex	$\hat{\sigma}^2_G$
10	♂♂	0·03195
20	♂♂	0·08161
25	♂♂	0·18898
28	♀♀	0·16263

Now, had the parents used for the progeny-tests been crossed at random within each line, $\hat{\sigma}^2_G$ would estimate half the true genetic variance. In fact, however, they were positively assortatively mated; if the assortative mating is perfect, *i.e.* if two identical genotypes are mated, then $\hat{\sigma}^2_G$ estimates the total genetic variance. Clearly, we have an intermediate situation here. Firstly, given that some genetic variation is present in the lines, mating has not been at random; and, secondly, it is highly unlikely that, for this

TABLE 4

Offspring/parent regression analyses within "Texas" inbred lines 10, 20, 25, 28

		♂♂		♀♀	
	d.f.	M.S.	P	M.S.	P
Line 10					
Between families	9	1·58000	N.S.	1·93556	N.S.
Regression	1	4·42220	5%–1%	0·00140	N.S.
Remainder	8	1·22472	N.S.	2·17732	N.S.
Pooled error	190	0·94105	—	1·23579	—
Line 20					
Between families	6	2·93334	5%–1%	0·79524	N.S.
Regression	1	2·25520	N.S.	1·94440	N.S.
Remainder	5	3·06896	5%–1%	0·56540	N.S.
Pooled error	133	1·30113	—	1·32030	—
Line 25					
Between families	7	5·60000	< 1%	2·21340	N.S.
Regression	1	9·48960	N.S.	1·35420	N.S.
Remainder	6	4·95174	5%–1%	2·35660	N.S.
Pooled error	152	1·82039	—	1·54901	—
Line 28					
Between families	14	1·87476	N.S.	6·42762	5%–1%
Regression	1	0·66440	N.S.	2·28000	N.S.
Remainder	13	1·96786	N.S.	6·74666	5%–1%
Pooled error	285	3·02912	—	3·17491	—

character, identical phenotypes are always genotypically identical. Thus mating has not been perfectly assortative at the genotypic level. The true genetic variance, therefore, is somewhere between $\hat{\sigma}^2_G$ and $2\hat{\sigma}^2_G$.

If we recall that the genetic variance in the "Texas" population from which these lines were derived is approximately 2·3 (see Experiment 1), we see that the variances observed here are, in comparison, greatly reduced. At worst, the inbreeding has resulted in the reduction of the genetic variance to one-sixth of its value (line 25) in the base population, and for lines 10 and 20 this reduction has been considerably greater. On average, however, the residual genetic variation is reduced 40-fold. The inconsistency with

which the genetic variance has reached significance in the two sexes further indicates the low level at which it exists in these lines. One may reasonably conclude, therefore, that the populations under study consist of individuals almost entirely homozygous at loci controlling chaeta number.

(c) *Selection in the cages*

The phenotypic variances (Vp) of adults emerging from the two experimental cages are shown in table 5. In both sexes, highly competitive larval

TABLE 5

Components of the phenotypic variances of adults from low and high densities

	♂♂			♀♀		
	$\hat{V}_A$	$\hat{V}_E$	$\hat{V}_p$	$\hat{V}_A$	$\hat{V}_E$	$\hat{V}_p$
Low	1·91847	2·72484	6·56178(500)*	2·76195	1·24459	6·76849(500)*
High	0·24297	1·04561	1·53155(407)*	0·00000	1·28364	1·28364(356)*

Note that, for the present inbred population, $V_p = 2V_A + V_E$.

* The number of flies scored.

conditions have resulted in a significant reduction in the phenotypic variance of adult chaeta number.

Analysis of the results of progeny-tests reveals that, in every comparable pair of regressions, the regression coefficient using parents from high density ($\hat{b}_H$) is significantly lower than that using low-density parents ($\hat{b}_L$) (table 6). This, together with the reduced phenotypic variance, indicates that there is considerably less genetic variance among high-density parents. Estimates of the additive genetic and environmental variances ($\hat{V}_A$, $\hat{V}_E$) among the

TABLE 6

Regression analysis from results of progeny-tests on adults from high (H) and low (L) densities

		Son on Father	Daughter on Father	Son on Mother	Daughter on Mother
Progeny mean ($\bar{x}$)	L	18·92	18·97	18·14	18·97
	H	19·10	20·19	19·29	19·96
$\hat{b}_L$	0·35714 ± 0·11963***	0·22679 ± 0·12037*	0·48214 ± 0·15848**	0·38214 ± 0·09322***	
$\hat{b}_H$	0·12857 ± 0·14722	0·17143 ± 0·09601*	0·05893 ± 0·15535	0·04643 ± 0·13054	

* = $p < 5\%$, ** = $p < 1\%$, *** = $p < 0{\cdot}1\%$.

survivors of high and low density conditions are shown in table 5, from which the reduction in genetic variance under competitive larval conditions is immediately apparent.

To compare the distributions of adults from the two cages, one must take into account any environmental depression in mean chaeta number at high density. Ideally, this depression can be estimated from the regression data, but this procedure depends upon homogeneity of the offspring/parent regression slopes for the two cages. Here, however, there is almost no genetic variance among the survivors at high density and, consequently, the

regressions are heterogeneous. In the absence of a direct estimate, the mean depression obtained in previous unpublished work (1 chaeta) has been used. That is, an individual which, when raised under the present high-density conditions, has a chaeta number x, would, on average, possess $(x+1)$ chaetae if raised in the present low-density cage. The high-density distribution of emergent adults must, therefore, be corrected by the addition of 1 hair to each observed phenotype.

The elimination of extreme phenotypes, in conjunction with the reduction in genetic variance, at high density shows that there has been selection, of a stabilising nature, of individuals with intermediate genotypes. We may proceed, then, to estimate phenotypic fitnesses, from the relationship

$$W_i' = f(P_{iH})/f(P_{iL})$$

where W_i' = relative fitness of ith phenotype,

$f(P_{iH})$ = frequency of ith phenotype at high density,

$f(P_{iL})$ = frequency of ith phenotype at low density.

These fitnesses, re-scaled so that W_i' (max) = 1·0, have been calculated separately for males and females, and the relationship between fitness and phenotype is illustrated in fig. 1 (*b*). In both sexes, the observed optimum is 18 chaetae, and fitness decreases rapidly, in a fairly linear manner, with increasing deviation, in either direction from this value.

In theory, a mechanism of single-locus overdominance for fitness can result in the selection of intermediate phenotypes, especially with multiplicative fitnesses and large selective disadvantages for homozygotes. However, it is unlikely that in the present populations, with very few loci segregating as compared to the " Texas " population, such a system of selection could account for the marked differences in phenotypic fitnesses. Since the experimental populations contain an unusually high frequency of homozygotes, it is much more likely that the selection observed has proceeded on the basis of homozygous differences between phenotypes; such a mechanism may be called selection for metric deviation. That is, in a normal population, with large numbers of both homozygotes and heterozygotes, subject to selection for metric deviation, two individuals with the same phenotype, but with quite different numbers of homozygous and heterozygous loci, may be equally fit. Furthermore, computer simulations suggest that with this type of selection, with fitnesses following a linear deviation model of the sort observed in the present experiment, genetic variance can be maintained in a randomly mating population (Gale and Kearsey, 1968; Kearsey and Gale, 1968).

It should be pointed out that heterozygous advantage and selection for metric deviation are not, of course, mutually exclusive forms of selection. There is no reason, in general, to suppose that, in populations containing extensive genetic variation, both should not operate. On the other hand, there is evidence that heterotic selection is not acting for chaeta number in populations of *D. melanogaster* derived from crosses between two inbred lines (Barnes, 1968; Killick, 1970). We suggest that it is not necessary for the type of relationship between a metrical character and fitness illustrated by fig. 1 (*b*).

4. General discussion

As has been stated elsewhere (Robertson, 1955), when we are dealing with a phenotype/fitness relationship for a metrical character, it is important to consider the possible ways in which the relationship can be produced. The relationships found here follow a similar pattern, both for males from the " Texas " population, and for each sex of the inbred population, (fig. 1). Moreover, females studied earlier, in the F_2 population derived from crosses between selection lines for high and low chaeta number (Kearsey and Barnes, 1970), again illustrate the distinct intermediate optimum and the sharp, linear decline in fitness with phenotypic deviation from this optimum. Any association, consequent upon artificial directional selection, between genes controlling chaeta number and subvital genes, cannot, of course, account for the array of phenotypic fitnesses observed in the " Texas " base population, which has been subject only to natural selection in the population cage. It may be argued that such association is responsible for the phenotype/fitness relationship among individuals from the F_2 population, but in view of the results of the two experiments reported here, this appears to be unlikely. In the case of the " Texas " population, we are certainly dealing with selection which is acting directly on genes controlling chaeta number. In the homozygous population this, too, is the most reasonable conclusion, unless we make the rather dubious assumption that, during the inbreeding to which the four lines have been subjected, deleterious genes have become fixed, by chance, to a greater extent in the two lines with the most extreme hair counts.

Given then, that selection is acting directly on genes controlling chaeta number, what can we say about the nature of this selection? In the case of the F_2 population, it is possible that intermediates were selected on a heterotic basis, *i.e.* differences in numbers of heterozygous chaeta loci may have accounted for the differences in relative fitnesses which were estimated. This explanation may also be proposed for the results from the base population. However, since for the largely homozygous inbred population the pattern of fitnesses (fig. 1 (*b*)) is as clearly defined, both in magnitude and in the shape of the graph, as that for the F_2 and base populations (fig. 1 (*a*)), the heterotic explanation as a major determinant for these relationships is rejected. Homozygous differences between individuals, at loci controlling chaeta number, appear to play a more important part in causing variation in fitness than do heterozygous differences. It is probable that this causal relationship is a result of pleiotropic gene action at the chaeta loci, and consideration of the environment in which the selection has been operating here suggests that genes at these loci contribute, to some extent, to larval competitive ability.

It is obviously important to discover if selection of the type and intensity found here is of widespread occurrence for other metrical traits. There is, however, no reason to expect chaeta number to be exceptional in terms of the intense selection to which it is exposed. On the contrary, prior to this series of experiments, chaeta number had been considered a peripheral character unrelated to fitness (Robertson, 1955, 1966). The mortality between egg and adult under our cage conditions is between 92 and 95 per cent., which is certainly sufficient to allow selective elimination of metric deviants for many other characters, while still allowing for a large degree of random loss.

5. Summary

1. Natural selection against extreme genotypes controlling sternopleural chaetae number has been demonstrated in two populations of *Drosophila melanogaster*. These were (i) a long-established cage population (" Texas ") and (ii) an artificial population comprising homozygous individuals derived from " Texas ".

2. The relationship between phenotype and fitness in both populations was essentially identical and closely resembled that found previously in a population derived from an F_2 between lines selected for chaeta number.

3. These results cannot be explained by the action of selection on subvital genes linked to loci controlling chaeta number.

4. It is concluded that selection is acting on the basis of metric deviation and not for heterozygosity *per se*.

5. Our results suggest that selection for metric deviation (stabilising selection) may be an important mechanism maintaining potential genetic variation for metrical traits in natural populations.

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