

Genetic differences between populations of *Drosophila melanogaster* for a quantitative trait

I. Laboratory populations

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SUMMARY

An experiment was carried out to test whether two laboratory cage populations of *Drosophila melanogaster* from different origins (Kaduna and Pacific) differed in the genes for sternopleural bristle number. The means, variances and heritabilities of the two populations and the synthetic formed from crosses between them were very similar.

Selection for low bristle number was practised in small replicate lines, six of each pure population and nine of the synthetic. On average, Pacific responded to selection rather more rapidly than either Kaduna or the synthetic, but there was little difference in the limit achieved.

Crosses between replicates within populations were made and selection continued, and these lines subsequently crossed between populations and reselected. Additional response was obtained by this procedure but the crosses between the replicates of the pure and synthetic populations attained similar selection limits.

An analysis of effects of individual chromosomes from the selected lines on bristle number indicated that the contribution of each chromosome to total response was about the same in Pacific, Kaduna and the synthetic.

It is concluded that differences in gene frequency, rather than the presence or absence of particular alleles, are mainly responsible for the differences observed between the populations.

1. INTRODUCTION

A large amount of research has been devoted towards ascertaining and understanding the genetic differences between populations from geographically distinct sources. Much of the work has been with *Drosophila* species and been concerned with readily observable variation, particularly polymorphisms producing electrophoretically different variants (e.g. O'Brien & McIntyre, 1969; Prakash, Lewontin & Hubby, 1969), but also chromosomal inversions (see Dobzhansky, 1970, for a review).

For two-allele polymorphisms, the general picture emerging from these studies is that populations differ in allelic frequencies, but specific alleles are not usually

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found in some populations which are completely absent from others. For loci with multiple alleles the situation can be regarded as one in which one or two alleles are segregating at reasonably high frequencies, and the other alternatives, which in some cases are numerous, are present at a small frequency in some populations and absent in others.

Much less is known about the genetic variation associated directly with quantitative traits, for simple comparisons of means and variances tell us nothing about the underlying gene frequencies at many loci. Some circumstantial evidence leading to conclusions similar to those of the enzyme polymorphism studies has been obtained by Milkman (1965, 1970), and information has been accumulated on geographical variation for quantitative traits, but without any attempt to explain this variation in terms of specific genetic effects (e.g. Prevosti, 1955; McFarquhar & Robertson, 1963; Anderson, 1968).

Animal breeders exploit genetic differences between breeds by planned cross-breeding, with the cross remade each generation from the parental breeds. They have also formed new breeds or strains by selecting within a crossbred base; but in the larger animal species, at least, the evidence for the merits of this practice is inadequate (see review by López-Fanjul, 1974). Successful incorporation of genetic material from different selected lines has been achieved by crossing to form a synthetic, and selecting within it, in *Drosophila* (Robertson, 1955; Osman & Robertson, 1968; Frankham, Jones & Barker, 1968), mice (Falconer & King, 1953; Roberts, 1967*a, b*) and poultry (Dev, Jaap & Harvey, 1969).

A cross between two populations will show at least as high a variance of gene frequency, $q(1-q)$, in the F_2 and subsequent generations as the mean variance, $\overline{q(1-q)}$, in the populations from which it derives (Wahlund's principle, 1928). Thus in a synthetic,

$$q(1-q) = \overline{q(1-q)} + \sigma_q^2,$$

where σ_q^2 is the variance in gene frequency between populations. For additive genes, the additive genetic variance behaves in the same way. Thus we should expect a synthetic to show higher initial variance and response to selection than the average of its parents if they differ at all in the frequencies of genes affecting the trait.

The increase in the additive variance of a synthetic as given by Wahlund's principle is only a property of a model of a single additive locus. Departures from additivity do not necessarily lead to an increase in variance in the F_2 . For loci showing complete dominance, the additive variance in the synthetic population from a two-way cross depends on the actual parental frequencies. If the mean frequency is less than about 0.5, when most variance is expressed, the synthetic has a higher variance than the parental mean (Lerner, 1954). When dealing with more than one locus the effect of linkage has to be introduced into the equations. For additive loci and the parental populations in linkage equilibrium, Wahlund's principle still holds, but in other cases no longer applies.

If a synthetic shows a higher initial variance than the parental average such an

observation gives us no information about whether there are genes segregating in one population which are completely absent from the other, or whether there are just small differences in gene frequency at many loci. For quantitative traits, the increase in the additive variance of an $F_2(V_{A2})$ compared to the average (\bar{V}_A) of two parental populations differing by an amount y_i in the frequency of n additive and unlinked genes of equal effect is

$$V_{A2} - \bar{V}_A = n(V_y + d^2/4n^2)/2,$$

where V_y is the variance of the y_i 's and d is the difference in mean ($d = 2\sum_i y_i$) between the two populations. If all y_i 's are equal, the difference $V_{A2} - \bar{V}_A$ is given by $d^2/8n$ (Wright, 1952). The formula shows that the greater the number of loci controlling the trait, the smaller the difference $V_{A2} - \bar{V}_A$ will be. Jackson & James (1970) show that the increment in variance in the cross is one-half of the variance between its constituent lines for additive genes in linkage equilibrium.

At the limit to selection, in a single locus model the chance of fixation of the favourable allele in a synthetic will be higher than the average chance of fixation in the parental populations whatever the gene action (Underwood, 1971). This is no longer so when several linked loci are considered. If selection were continued to a limit in a very large population so that all favourable alleles were fixed, the same limit would be achieved in the pure populations and in the synthetic provided the differences between the parental populations were only differences in gene frequencies. However, the limit achieved in the synthetic would exceed that in its parents if some useful genes were present in each of the parental populations that were absent in the other.

A test of relative response and limit has been applied to two *Drosophila* cage populations (Kaduna and Pacific) and the synthetic from the cross between them, using sternopleural bristle number as the trait. The results are described in this paper. It is, of course, impossible in practice to maintain the selected populations of sufficient size to ensure fixation of all favourable alleles, but we have kept them as large as labour permitted. For as A. Robertson (1960) has shown, the limits to selection depend on the intensity of selection and the population size as well as the basic properties of the initial population. Rather than using a single large selected line of each population from the outset, we established several small lines and subsequently crossed them after some generations of selection. This should give the same limits as using a large population throughout if gene effects are additive (Maruyama, 1970), but may be more efficient if recessive alleles are favoured (Madalena & Hill, 1972).

2. MATERIALS AND METHODS

The Kaduna population was captured in Nigeria (Clayton, Morris & Robertson, 1957) and the Pacific on the west coast of the United States (F. W. Robertson, 1960, personal communication). Both had been maintained in cages in this laboratory at 25 °C for many years before this experiment was started by taking

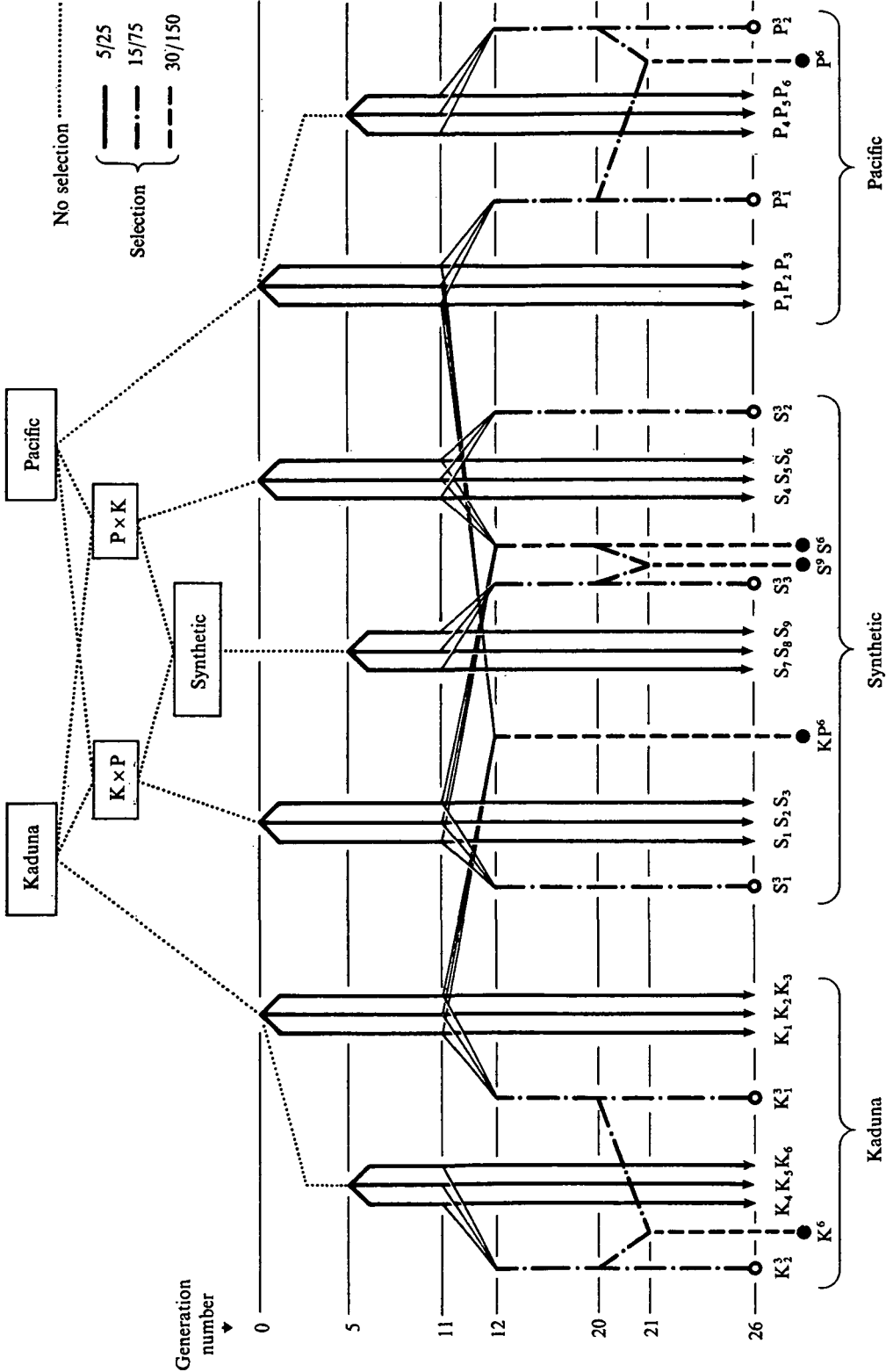


Fig. 1. The experimental design.

a sample of eggs from each cage. The flies which hatched from these and all subsequent generations were cultured in half pint milk bottles at 25 °C, except those of generations 13, 24, 35 and 45 which were cultured at 18 °C. Using a sample of eggs from the cages, over 200 of the flies hatching were used to make each reciprocal cross between the two populations. These constituted the first synthetic base population. The F_1 reciprocal crosses were mated and maintained without selection as the synthetic source material.

In all lines under selection the 20 % of flies recorded of each sex with the lowest number of bristles on the two sternopleural plates were selected. When a cross between k lines, each of size N , was made, the selected 20 % of both sexes from each line were put into the same bottle and subsequently maintained with size kN , subject to a maximum of 150 males and 150 females, and under the same selection intensity.

The design of the experiment and line designations are shown in Fig. 1. At generation 0 three replicate lines of Kaduna (K_1, K_2, K_3), three of Pacific (P_1, P_2, P_3) and three of each of the F_1 reciprocal crosses, Kaduna \times Pacific (S_1, S_2, S_3), and Pacific \times Kaduna (S_4, S_5, S_6), were started, and 5/25 of each sex selected each generation (i.e. 5 selected from 25 scored). At generation 5 a further set of 9 lines was initiated from the populations maintained in bottles, namely three Kaduna (K_4, K_5, K_6), three Pacific (P_4, P_5, P_6) and three Synthetic (S_7, S_8, S_9), and again 5/25 of each sex subsequently selected. At generation 11 crosses were made between replicates within populations and sets (i.e. time selection started). These seven lines (denoted by a superscript 3) were subsequently selected with intensity 15/75. The lines are K_1^3 (from the cross of K_1, K_2 and K_3 , the first set of Kaduna lines), $K_2^3, P_1^3, P_2^3, S_1^3, S_2^3, S_3^3$ as shown in Fig. 1. Also at generation 11, crosses were made between 6 lines of the first set of replicates, KP^6 between the pure lines and S^6 between the synthetics. Higher order crosses were also made as follows: at generation 20 crosses were made between the three way crosses of generation 11, to form K^6, P^6 and S^9 , and selected with intensity 30/150 for 13 generations and 15/75 subsequently; at generation 31, KP^6 and S^6 were crossed to give KPS^{12} , selected at 30/150; at generation 38, K^6 and P^6 were crossed to give KP^{12} ; and at generation 42, KP^{12} and S^9 were crossed to give KPS^{21} . These latter lines are not shown in Fig. 1; both were selected with intensity 15/75.

With the design employed comparisons of rates of response and limits could be made between lines of different sizes from different populations, and the strategy of crossing the populations to form synthetics early (lines S) compared with that of crossing after selection (lines KP).

Lines were relaxed at several stages of selection. Some further relaxation tests were performed on lines showing aberrant response patterns. In an attempt to reduce crowding effects in these lines, the available females were allowed to oviposit for only 7 h in a bottle.

Chromosomal analysis. Tests of effects of different chromosomal substitutions on bristle scores in some lines were undertaken using the technique of Osman & Robertson (1968). Males from a stock with a dominant marker on each autosome

(Pm, Sb, ci^D) were crossed to females of the line to be analysed. Male offspring carrying all three markers were crossed again to females of the line, and the bristle scores recorded on 10 males and 10 females of each of the 8 different genotypes in the progeny of the second cross.

3. RESULTS

(i) *Base populations*

The means and variances of the base populations maintained in bottles are shown in Table 1. There is no consistent difference between the mean of Pacific and Kaduna, and the synthetic slightly exceeds their mean. On average, the synthetic shows a higher variance than either parent. Both the means and

Table 1. *Means, variances and coefficients of variation (CV) for the unselected base populations maintained in bottles*

Genera- tion	Kaduna			Pacific			Synthetic		
	Mean	Vari- ance	CV (%)	Mean	Vari- ance	CV (%)	Mean	Vari- ance	CV (%)
0	18.07	3.69	10.6	18.29	4.04	11.0	18.29	4.36	11.4
5	17.03	2.73	9.7	17.03	4.38	12.3	17.23	2.98	10.0
8	17.42	3.13	10.2	17.02	3.14	10.4	17.50	3.67	11.0
15	17.06	2.80	9.8	16.65	3.07	10.5	17.46	3.80	11.2
20	16.53	3.02	10.5	17.10	2.91	10.0	17.09	3.25	10.5
25	16.41	2.60	9.8	16.44	2.71	10.0	16.79	3.63	11.3
32	16.70	2.69	9.8	16.17	2.12	9.0	17.07	3.17	10.4

Table 2. *Heritabilities of the base populations with standard errors*

(i) Estimated by offspring on mid-parent regression

Kaduna	Pacific	Synthetic
0.39 ± 0.05†	0.40 ± 0.07	0.54 ± 0.08‡ 0.45 ± 0.05§ 0.47 ± 0.04 (Pooled)

(ii) Realized heritabilities over the first three generations of selection ||

	Kaduna	Pacific	Synthetic
1st set of lines	0.37 ± 0.09	0.42 ± 0.05	0.42 ± 0.03
2nd set of lines	0.28 ± 0.07	0.38 ± 0.05	0.26 ± 0.03
Pooled estimate	0.33 ± 0.05	0.40 ± 0.04	—

† From Madalena (1970).

‡ After five generations of random mating.

§ After 20 generations of random mating.

|| Standard errors corrected for drift (Hill, 1972).

variances of each line show a downward trend over 32 generations, unassociated with any known culture changes. Similar results were observed in the control lines from the Kaduna population kept in bottles by Clayton and Robertson (1955, 1964).

Heritabilities estimated by regression of offspring on mid-parent and by realized heritability in the first three generations of selection are shown in Table 2. The design used to estimate the regression coefficients included assortative mating of the parents to increase the statistical precision of the estimate (Reeve, 1961). For the synthetic the design included divergent selection in the parents, again to reduce further the standard errors of the heritability estimates (Hill, 1970). Although the heritability estimate for the synthetic was higher than for Pacific and Kaduna using offspring on mid-parent regression, this difference was not significant, and the realized heritability estimates did not show the same pattern. The two sets of realized heritability estimates from the synthetic were heterogeneous, the second set giving a low estimate. Apart from this, there was fair agreement between the two kinds of heritability estimate.

(ii) *Small replicate lines*

The five-generation moving average scores of the small replicate lines (5/25) are shown in Figs. 2, 3, and 4 for Kaduna, Pacific and synthetics respectively. The scores are plotted by generation of selection, so the first and second sets of repli-

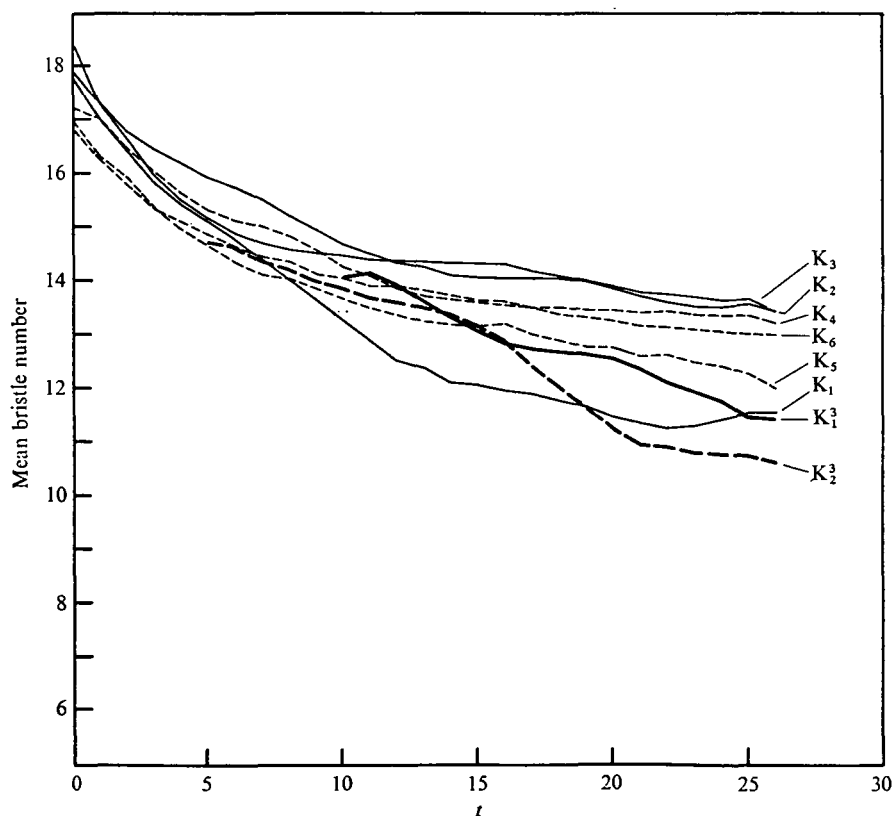


Fig. 2. Scores on Kaduna replicates and their three-line crosses (five generation moving averages). Scores for K_1^3 at generations 5 and 6 are the means of its parental lines K_1 to K_3 and scores for K_2^3 at generations 10 and 11 are means of K_4 to K_6 .

icates are not contemporaneous. There is considerable variability between replicates, for example line P_2 responded by three bristles in generations 14–17. In general, however, about half the total response was made in the first five generations, with only a small additional response after ten generations. A plateau had essentially been reached when selection was terminated at generation 26.

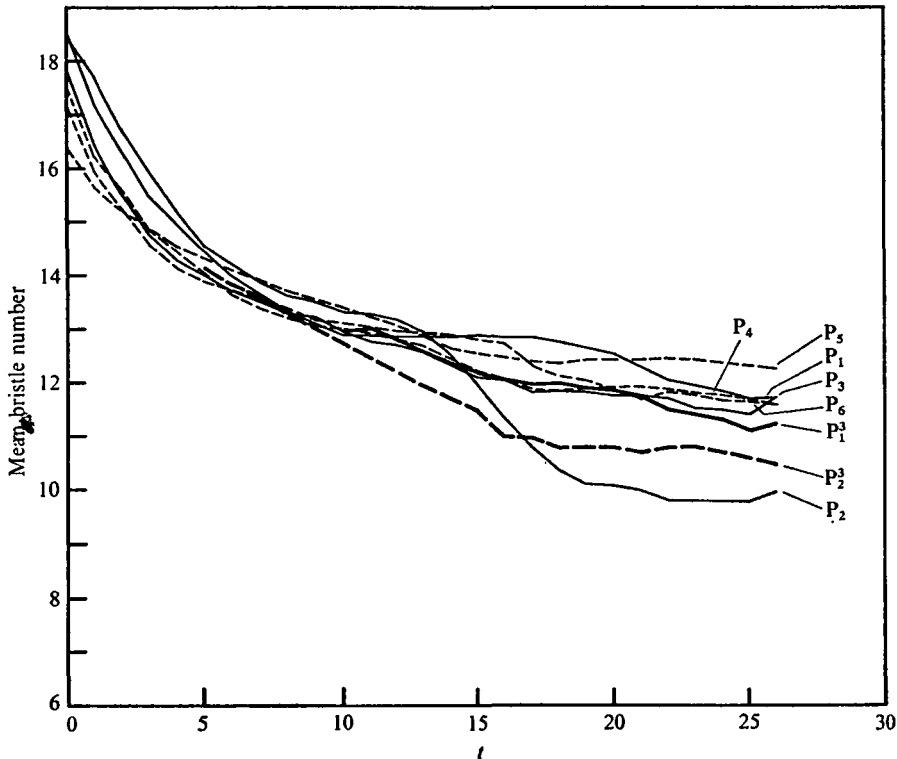


Fig. 3. Scores on Pacific replicates and their three-line crosses (five generation moving averages). Scores for P_1^3 at generations 5 and 6 are the means of its parental lines P_1 to P_3 , and scores for P_2^3 at generations 10 and 11 are means of P_4 to P_6 .

The mean scores of lines drawn from each base population are shown in Fig. 5 for the first set of lines and in Fig. 6 for the second set. The two groups of synthetic replicates formed from the reciprocal crosses $K \times P$ (S_1, S_2, S_3) and $P \times K$ (S_4, S_5, S_6) in the first set did not differ consistently in performance, so the mean of all six lines is given in Fig. 5. In both the first and second set of lines there was, on average, both a more rapid initial response and higher limit (i.e. fewer bristles) in Pacific than Kaduna. However, the synthetic lines of the first set showed an initial response and limit intermediate between those of Pacific and Kaduna; those of the second set initially responded at a similar rate to Kaduna, but finally reached an intermediate position. For a few generations, mean, variances and coefficients of variation of bristle score are given in Table 3 with averages taken over replicates. The variances declined to about 40% of their original value during

the first five generations and fell slightly thereafter, but the coefficients of variation showed much less change. This reduction in the variance of the selected lines was more marked than the value of about 9% predicted for a model of additive genes of very small effect with infinite population size (Bulmer, 1971). Throughout, the Pacific lines showed, on average, higher variances and coefficients of variation than either the Kaduna or synthetic lines.

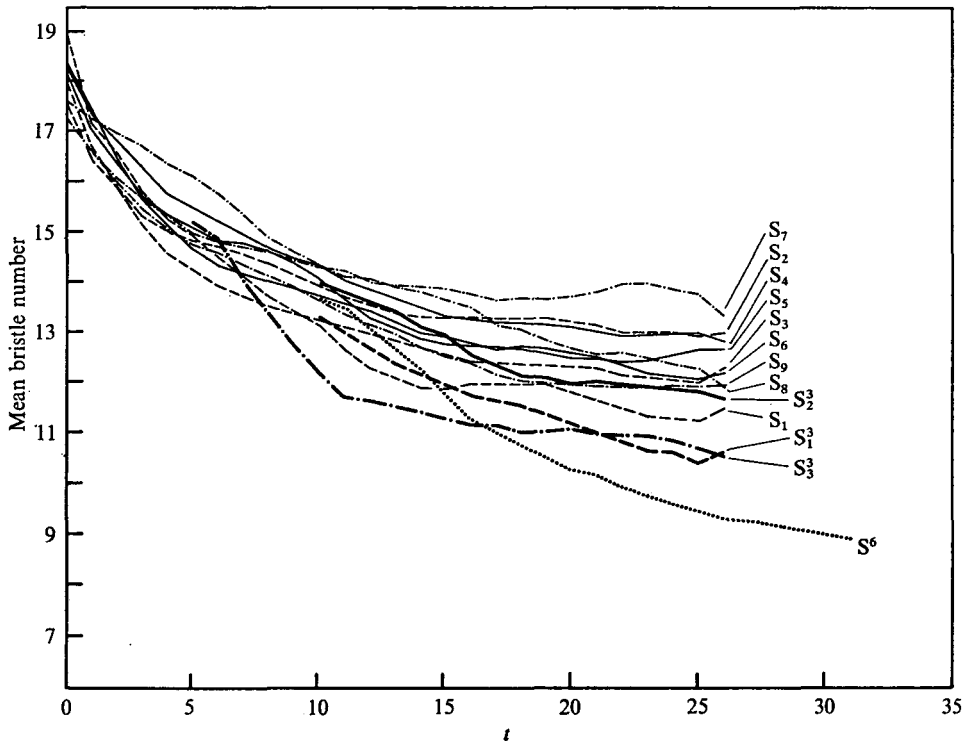


Fig. 4. Scores on the synthetic replicates and their three-line crosses (five generation moving averages). Scores for S_2^3 and S_3^3 at generations 5 and 6 are the means of their parental lines S_1 to S_3 and S_4 to S_6 , respectively, and scores for S_3^3 at generations 10 and 11 are means of S_7 to S_9 .

(iii) *Lines from crosses between small replicate lines*

Bristle scores resulting from selection in the lines of size 15/75 each formed from the crosses of three small lines are shown in Figs. 5 and 6, and some variances and coefficients of variation in Table 3. The crosses were made at generation 11 for the first set and generation 6 for the second set, so the cross lines are contemporaneous. The results of further selection in higher-order crosses, involving six or more small lines or two or more of the lines based on three-way crosses are given in Figs. 5–7 and Table 3.

All three-way crosses responded to subsequent selection and eventually attained similar mean scores regardless of origin, although those of the first set of lines still showed some response when selection was terminated. There was little change in

the coefficients of variation except in S_3^3 . The realized heritability of the crosses over the first three generations of selection was smaller than that estimated over five generations, as shown in Table 4. The highest-order crosses showed further response over their parent lines, as did all crosses among replicates with the

Table 3. Means, variances and coefficients of variation (CV) for selected lines at different generations

Line	Mean				Variance				CV (%)			
	1	5-6	10-11	20-21	1	5-6	10-11	20-21	1	5-6	10-11	20-21
K†	17.6	15.2	14.0	13.1	3.45	1.60	1.44	1.39	10.6	8.1	8.5	8.8
P†	17.7	14.3	13.1	11.8	4.10	1.89	1.72	1.52	11.5	9.4	9.8	10.3
\bar{S} †	17.9	15.1	13.7	12.7	3.78	1.65	1.31	1.23	10.7	8.4	8.3	8.6
K_1^3	14.3	12.7	12.4	—	1.58	1.66	2.16	—	8.8	10.1	11.8	—
P_1^3	13.3	12.0	11.8	—	2.71	1.89	2.02	—	12.4	11.4	12.0	—
S_1^3	14.0	12.7	12.0	—	1.60	1.44	1.21	—	9.1	9.4	9.1	—
S_2^3	13.3	11.8	11.1	—	1.61	1.39	1.13	—	9.7	9.9	9.5	—
K_2^3	14.8	13.7	13.1	10.8	1.77	1.06	1.45	1.27	8.9	7.5	9.2	10.5
P_2^3	13.9	12.5	11.3	10.6	1.67	2.10	1.20	1.67	9.5	11.6	9.7	12.2
S_3^3	15.1	11.9	11.3	10.7	2.01	2.63	2.51	2.37	9.4	13.6	14.0	14.4
K^6	12.9	11.6	10.7	8.8	1.57	1.75	1.73	1.47	9.7	11.4	12.5	13.7
P^6	11.7	11.0	10.4	8.5	1.81	1.45	1.44	0.74	11.5	10.9	11.5	10.1
S^6	13.4	11.4	10.3	9.0	2.28	1.63	2.26	1.28	11.0	11.1	14.6	12.5
KP^6	13.7	12.2	9.8	8.9	1.76	2.01	1.79	1.29	9.9	11.6	13.6	12.7
S^9	10.6	9.6	9.4	7.5	2.30	1.61	1.92	3.55	14.3	13.3	14.6	25.1
KPS^{12}	8.7	7.4	5.8	—	2.09	3.40	3.45	—	16.5	24.8	31.5	—
KP^{12}	8.8	7.7	7.1	—	0.95	0.74	0.93	—	11.0	11.1	13.5	—
KPS^{21}	7.4	5.4	3.9	—	2.24	3.40	3.45	—	20.5	34.2	47.9	—

† Generations 0 and 4-5 rather than 1 and 5-6. Mean of 6 (K, P) or 9 (\bar{S}) sublines.

exception of K_1^3 and P_1^3 , which did not exceed their best parent. Usually about 5 generations were taken to exceed the best parent, or up to 10 if these were already three-way crosses with a low mean. The combined lines P^6 , K^6 and S^9 achieved a similar response until very late in the selection (25 generations from the formation of K^6 or 46 from the start) when K^6 showed an accelerated response. The final limits achieved of five or fewer bristles are very low scores for *Drosophila* selection experiments (cf. Osman & Robertson, 1968). A summary of the level reached in each line when selection was terminated is given in Fig. 8. Taking these as selection limits, it appears that the limit depended more on the size of the line than on its source population. There was only a small difference in favour of S^9 , from selection within crossed populations, over KP^{12} , from crossing selected populations followed by further reselection.

(iv) Relaxation of selection

The effects of relaxation of selection are shown in Table 5. These values show the difference between the performance of the line after it has undergone the specified number of generations of selection and its performance after five subse-

quent generations of relaxation. In this comparison it is assumed there were no environmental trends over the five generation period. Only those single lines (P_2 , P_3 and P_6) with a significant upward trend on relaxation are listed; these lines all showed greater response than the average of those from the same popula-

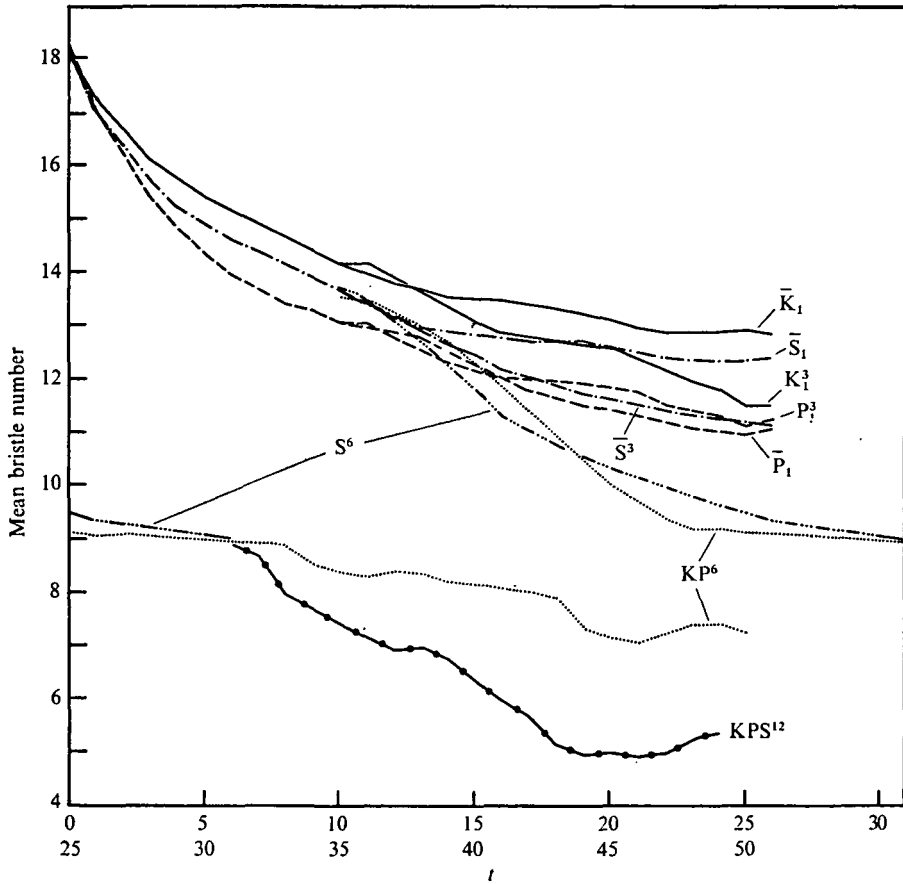


Fig. 5. Mean scores of the first set of replicate lines and scores on crosses derived from them (five generation moving averages). Generations 25-50 refer to S^6 , KP^6 and KPS^{12} only.

tion. All of them are from the Pacific whose replicate lines achieved the lowest means. Relaxation effects were found in at least one three-way cross from each population, and in all higher way crosses. It is noteworthy that of the small lines or three-way crosses, P_2 , P_3 and S_3^3 had all shown increased variances for sternopleural bristle number in later generations. Apparently genes with deleterious effects on fitness are being selected in each population.

(v) *Chromosomal analysis*

Least-squares estimates for the effects of the markers (Pm, Sb and ci^D) when substituted into the different lines are given in Table 6, together with the effect of these markers in crosses between females of a line and marked males from the

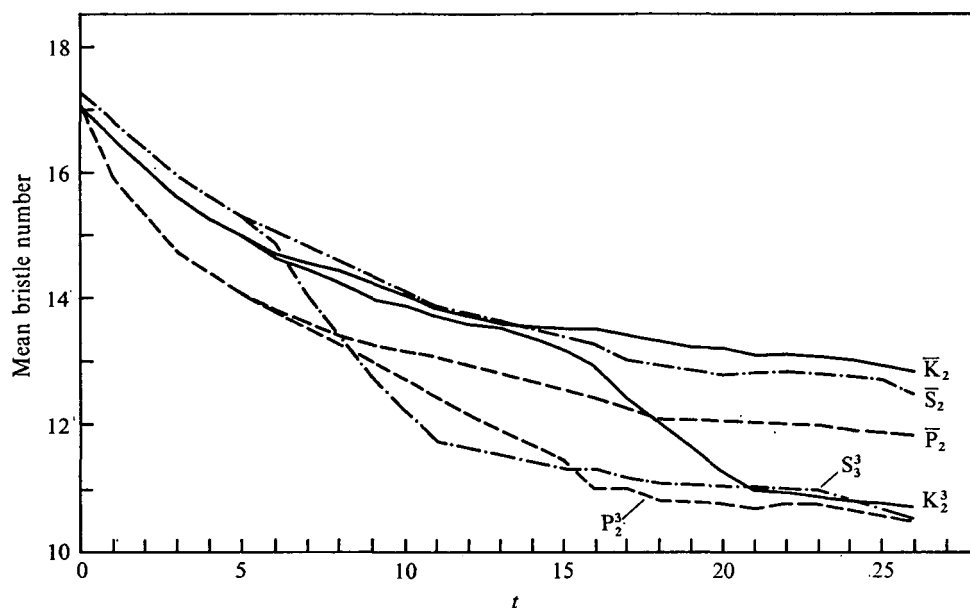


Fig. 6. Mean scores of the second set of replicate lines and scores on crosses derived from them (five generation moving averages).

Table 4. *Realized heritabilities of the crosses*

Line ...	K_1^3	K_2^3	P_1^3	P_2^3	S_1^3	S_2^3	S_3^3	
h^2 over 3 generations (1)	0.06	0.13	0.06	0.13	0.09	0.19	0.32	
h^2 over 5 generations (2)	0.19	0.18	0.13	0.18	0.14	0.22	0.40	
Line ...	K^6	P^6	S^6	KP^6	S^9	KP^{12}	KPS^{12}	KPS^{21}
h^2 over 3 generations (1)	0.27	0.09	0.10	0.09	0.17	0.24	0.21	0.43
h^2 over 5 generations (2)	0.21	0.19	0.15	0.24	0.18	0.21	0.22	0.24

Standard errors corrected for drift (Hill, 1972).

(1) Average = 0.06 (range 0.03–0.13).

(2) Average = 0.04 (range 0.03–0.09).

other two. None of the interactions between chromosomes were significantly different from zero and the results are not listed. Although most estimates of effects differed significantly from zero, those from alternative crosses usually did not differ

by a significant quantity from each other. The crosses to the marker stocks were made at generations 27 and 28 and preceded the late response in K⁶ (Fig. 7). Mean bristle number was found to increase in these three lines when relaxed and this is confounded with the effects of the markers on bristle score.

Table 5. *The effect of five generations of relaxed selection on bristle score*

(Positive values denote an increased bristle score, or relaxation effect. The first (second) generations shown are those when relaxation commenced (ended). The final mean is that value ultimately reached by the line with continued selection.)

	Generations				Final mean
	10-15	15-20	20-25	25-30	
Single replicates showing significant effects					
P ₂	—	—	1.70**	1.58**	9.98
P ₃	—	—	0.64*	1.00**	11.68
P ₆	—	0.58*	0.56*	0.90**	11.58
Mean of all single replicates					
K	—	-0.57†	0.14	0.03	12.81
P	—	0.35†	0.59	0.74	11.47
S	—	0.11†	-0.08	-0.08	12.43
All three-way crosses					
K ₁ ³	0.53	0.48	—	—	11.48
K ₂ ³	—	0.38	0.72**	—	10.64
P ₁ ³	1.34**	0.43	—	—	11.21
P ₂ ³	—	0.21	0.79**	—	10.43
S ₁ ³	-0.22	0.34	—	—	11.70
S ₂ ³	—	0.11	—	—	10.59
S ₃ ³	—	1.38*	2.05*	—	10.55
All higher-order crosses					
K ⁶	—	—	1.06**	—	5.23
P ⁶	—	0.85**	1.18**	—	7.97
S ⁶	1.83**	1.43**	2.84**	—	8.92
KP ⁶	0.96**	1.13**	0.99**	—	8.93
S ⁹	—	1.06**	2.20**	—	6.65

—, Not available.

* $P < 0.05$; ** $P < 0.01$.

† Only the second set of lines scored in generations 15-20, i.e. K₄, K₅, K₆, P₄, P₅, P₆, S₇, S₈, S₉.

The chromosome effects of the lines are compared in Table 7, and estimates of the amount of heterosis (the difference between crossbred and pure bred means) and the degree of heterosis (the amount of heterosis as a proportion of the difference between the pure bred means) are also included. Although the degrees of heterosis have large standard errors they sometimes exceed unity, indicative of either overdominance or complete dominance in which the dominance genes fixed in each line are different. It should be noted that *dominance* for bristle score implies that *recessive* genes are favoured by selection for low bristle number.

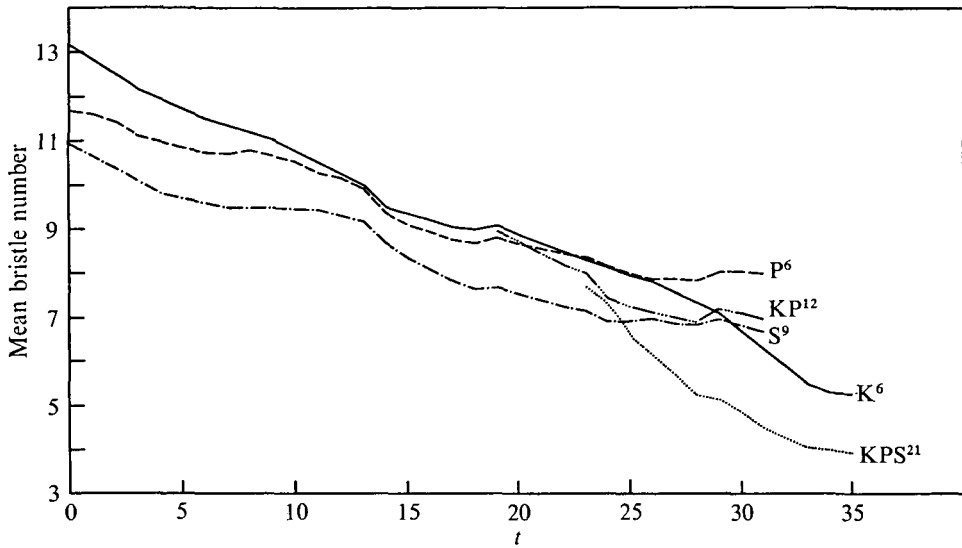


Fig. 7. Scores of the higher-order crosses (five generation moving averages). Generation 0 for these lines corresponds to generation 19 from the start of the first set of replicates.

Table 6. *Estimates of chromosomal effects on bristle number relative to the marker stock*

δ/φ	Chromosome								
	II			III			IV		
	K ⁶	P ⁶	S ⁹	K ⁶	P ⁶	S ⁹	K ⁶	P ⁶	S ⁹
K ⁶	0.67	0.62	1.06	0.70	0.72	0.80	0.45	0.70	0.37
P ⁶	0.69	0.86	0.79	0.69	1.26	1.21	0.74	0.69	0.46
S ⁹	1.17	1.62	0.72	0.65	0.92	1.05	0.05	0.35	0.50

Significance levels

Single effect > 0

Difference between two effects > 0

$P < 0.05$

$P < 0.01$

0.16

0.20

0.22

0.29

Table 7. *Paired comparisons of lines in terms of differences in estimates of effects of individual chromosomes on: pure performance (e.g. $K-P = -[(K^6 \times K^6 - P^6 \times K^6) + (K^6 \times P^6 - P^6 \times P^6)]$), amount of heterosis (e.g. $KP = \frac{1}{2}(K^6 \times P^6 + P^6 \times K^6) - \frac{1}{2}(K^6 \times K^6 + P^6 \times P^6)$) and degree of heterosis (e.g. $D_{KP} = |KP/(K-P)|$)*

Chromo- some	K-P	KP	D_{KP}	K-S	KS	D_{KS}	P-S	PS	D_{PS}
II	0.26	-0.11	0.4	0.16	0.40	2.5	0.69	0.41	0.6
III	0.53	-0.27	0.5	0.20	-0.15	0.7	-0.50	-0.09	0.2
IV	0.28	0.15	0.7	-0.27	-0.26	1.0	-0.30	-0.19	0.6
S.E.	0.34	0.17		0.34	0.17		0.34	0.17	

A similar analysis was performed on line KPS²¹ after nine generations of selection following its formation, and the effects of the markers are shown below, each with a standard error of 0.28:

Effect	Chromosome						
	II	III	IV	II × III	II × IV	III × IV	II × III × IV
Effect	2.01	0.91	1.19	0.36	0.14	0.14	0.54

Chromosome III scored similarly to that of its parental lines P⁶, K⁶ and S⁹ (Table 6) but the effects of chromosomes II and IV were more than double those estimates. The third-order interaction was just significant ($P \sim 0.05$), but the interaction disappeared if a logarithmic transformation of the data was performed, a method recommended by McPhee & Robertson (1970) for reducing the effects of background genes on the substitutions of interest.

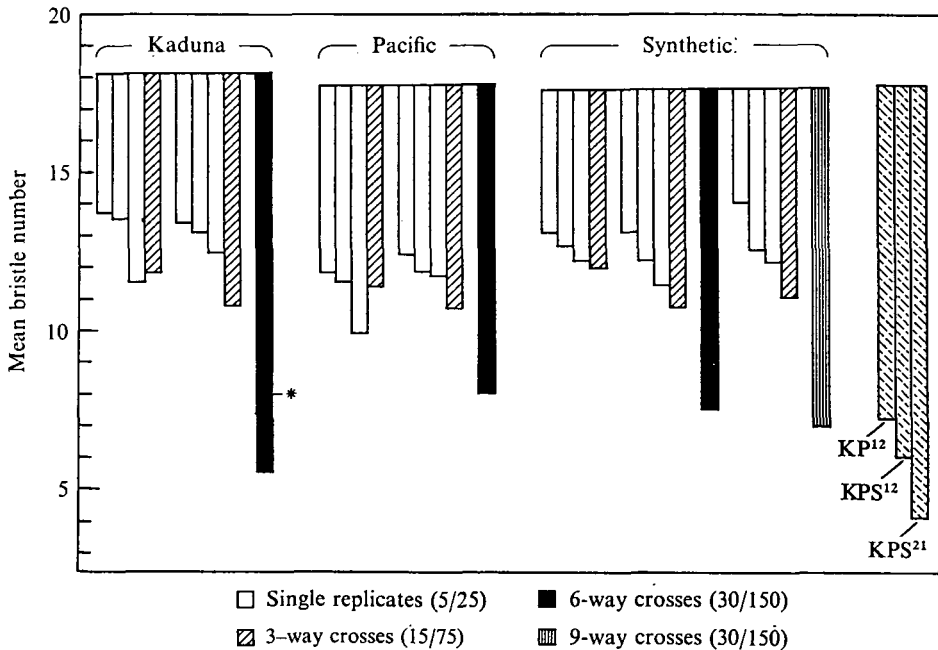


Fig. 8. Limits reached by different lines, calculated from the mean performance over the last five generations of selection in each. (*Level of K⁶ prior to the delayed response at generation 27.)

4. DISCUSSION

Although the difference between the Kaduna and Pacific replicate lines in their mean response to selection was small, there was a fairly consistently higher rate of response in Pacific. Thus there was some evidence of differential gene frequencies for sternopleural bristle numbers. However, the synthetic lines responded at about the same rate or slightly less than the average for Pacific and Kaduna lines, and under most simple models a higher rate of response would be predicted for

the synthetic if there were differences in gene frequency between the parents, as we discussed earlier in the paper. It is very difficult to estimate the selection limit with any precision, and due to limitation of population size favourable genes were presumably lost by chance from all the lines constituting the largest Pacific, Kaduna and synthetic lines (P^6 , K^6 and S^9). Nevertheless, our results suggest that similar limits were achieved in each case. There are some complications however, for example the late response in K^6 , but in selection experiments for bristle number in *D. melanogaster* peculiar response patterns, probably due to initially rare genes of large effect, are often encountered (Clayton *et al.* 1957; Madalena, 1970).

Accelerated responses to selection occurred in a number of lines. Some of those responses immediately followed the formation of a cross and they can be attributed to the presence of genetic differences between the parental lines (S_3^3 , KPS^{12} and KPS^{21}). Other lines showed a delayed response to selection after a period of relative stability (P_2 , K^6 and S^9). Whether those delayed responses are due to rare cross-overs, favourable recessives at an initially low frequency, mutation or modifications of the back-ground genotype is not known. However, the occurrence of such unpredictable events does not affect the comparison between pure and synthetic lines except in introducing more noise. It is hoped to present an analysis of some of these aberrant responses in a separate paper.

Realized heritabilities measured over three generations of selection in the crosses between replicates were usually smaller than those estimated over five generations. This would conform with theoretical predictions of negative linkage disequilibrium between the selected replicates (Robertson, 1970). The initial delay in the response of the crosses may also be due to the presence of favourable recessive alleles in the parental lines. This recessive gene action would be masked by crossing the lines thereby slowing the response of the cross for some generations, and would explain why crosses needed a number of generations to surpass the average of the parental lines, also under selection. Deleterious alleles with an effect on the selected trait, most of them presumably recessives, were present in all higher order crosses, as revealed by changes in the selected lines under relaxation.

The similarity of selection limits (Fig. 8) is evidence that the Pacific and Kaduna populations were segregating for the same genes. It is possible that the initial differences in response between the two populations were associated with a small difference in mean gene frequency, such that the additive variance was rather higher in Pacific. For example, with additive genes, Pacific might have frequencies (for low bristle score) of around 0.5 and Kaduna around 0.4. However, unless all loci have these frequencies, the synthetic might show larger variance, for these values would otherwise represent mean frequencies. The other criticism of the hypothesis is that the original mean scores of Pacific and Kaduna were very similar.

Notwithstanding detailed discussion of possible models, there remains the problem of understanding why the two populations, captured from widely different geographical sources, are so similar. There are at least three alternative hypotheses: (1) that the populations were just as similar when they were originally

captured, (2) that they have changed by natural selection to essentially the same population in order to adapt to the laboratory environment, and (3) that the populations have become contaminated in the laboratory. We cannot provide evidence on these alternatives with the data available. In a following paper (López-Fanjul & Hill, 1973) we report an experiment designed to obtain further information on these possibilities.

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