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Artificial selection with differing population structures

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SUMMARY

The effect of subdivision of a population on response to artificial directional selection for abdominal bristle number in *Drosophila melanogaster* was compared using large, replicated lines. Three different population structures were compared: (i) selection in an Undivided, large population with 50 pairs of parents (treatment U); (ii) selection in each of 10 sublines which were reconstituted every 6th generation by Crossing after Culling the 5 lowest sublines (treatment CC); and (iii) selection in each of 10 sublines which were reconstituted every 6th generation by Crossing after Retaining all 10 sublines (treatment CR). At the end of three cycles of selection and crossing, neither CR nor CC was superior to U; sublining did not increase response to selection. These results agree with the predictions arising from an entirely additive model and provide no evidence for the presence of epistasis.

A comparison of 50-pair lines (U) with several 5-pair lines was made over 31 generations. For the 50-pair lines, there was close agreement between response predicted from the base population (using $ih^2\sigma_P$) and observed response throughout all 31 generations of selection. Although the best of the 5-pair lines exceeded the 50-pair lines in the early generations, average response to directional selection in the 5-pair lines soon fell behind that predicted from $ih^2\sigma_P$, and soon reached a plateau.

1. INTRODUCTION

The importance of population structure in determining the success of artificial selection programmes was first discussed by Wright (1922*c*). Having been greatly impressed by the results of early experiments on inbreeding and crossing in plants and animals generally (East & Jones, 1919) and particularly in guinea pigs (Wright, 1922*a*, 1922*b*, 1922*c*), Wright (1922*c*) concluded that improvement in livestock would be more rapid if a population was subdivided into small lines, with regular crossing and selection among lines, than if the population was kept as one undivided line. The validity of this conclusion was reinforced in Wright's mind by the results of his investigation into the breeding history of Shorthorn cattle (Wright, 1923*a*, 1923*b*; McPhee & Wright, 1925), which indicated that the improvement in these cattle throughout their recorded history resulted not

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from mass selection in one large population (that is, the whole breed), but from selection within and between partially isolated and relatively small populations (that is, herds and/or strains within the breed).

Subsequently, Wright (1929, 1931, 1932; and reviewed in 1977*a*, 1978) applied the same ideas to evolution in natural populations, concluding that evolution would be much more rapid in a subdivided population with occasional diffusion (migration) among lines than in an undivided population, but only if there were considerable epistasis with respect to fitness.

The ideas expressed by Wright (1922*c*, 1929, 1931, 1932) were further developed and widely publicised in the context of artificial selection by Lush (1937, and later editions) who strongly recommended subdivision of a population into small lines, and artificial selection within each line, with periodic selection among lines and crossing of remaining lines. Wright (1939) reinforced this recommendation.

Because of the theoretical and practical importance of this recommendation, its effectiveness has been tested in simulated populations and in various laboratory populations. The simulation studies conclusively showed that if gene action is entirely additive with respect to overall fitness, then the fastest and greatest response to artificial directional selection will be obtained in an undivided population (Madalena & Hill, 1972), except in the very short term, when the best subline may be superior to the undivided line for just a few generations (Baker & Curnow, 1969; Madalena & Hill, 1972).

Selection experiments in mice by Bowman & Falconer (1960), in *Tribolium* by Enfield (1970), Goodwill (1974), and Katz & Enfield (1977), and in *Drosophila* by Hill (1963) and Madalena & Robertson (1975) have produced results similar to those with simulation. In all cases, there was no real advantage to be gained from subdivision. The only experiment to indicate superiority of subdivided lines has been the *Drosophila* selection programme conducted by Katz & Young (1975). To the extent that the design and aims of this experiment were different from those others listed above, its results are not directly comparable with the results of the other experiments. Katz & Young's experiment does, however, raise some doubts as to the generality of conclusions drawn from other experiments, especially in *Drosophila*.

This paper reports the results of a replicated experiment undertaken in *Drosophila* to examine the effect of population structure on response to artificial directional selection.

2. MATERIALS AND METHODS

(i) *Introduction*

Artificial directional selection was conducted for increased abdominal bristle number in the Canberra strain of *Drosophila melanogaster*. Fast and accurate scoring of bristle number was made possible by using a population that was homozygous for *scute*[1], which considerably reduces bristle number without altering any other parameters of the population (Rathie, 1969). The character selected was bristle number on one abdominal segment (fourth in males and fifth

in females), these being the segments most easily scored. There is an estimated genetic correlation of 1·0 between fourth and fifth abdominal segments in each sex in the Canberra wild type strain (Sheridan *et al.* 1968) and in the Canberra *scute*[1] strain (Hammond, 1973). In the base population used for this experiment, mean abdominal bristle number was 8·15, with a phenotypic standard deviation of 1·58 (Rathie, 1969), and a heritability of 0·20 (Hammond, 1973).

Generation interval was always 14 days, and parents were left in vials for 3 days before being discarded. For generations 0 to 16 inclusive, all lines were perpetuated by single-pair matings in 3 × 1 inch glass vials. Thereafter, all flies were kept in five-ounce cream bottles. A single bottle was used for 5-pair lines, and larger lines had 10 pairs of parents per bottle. The culture medium was a dead yeast fortified medium (medium F of Claringbold & Barker, 1961), seeded with a small amount of live dried yeast. All cultures were maintained at a temperature of 25 ± 0·5 °C and at a relative humidity of 65–70 %, in a room lit for 12 h daily (6 a.m. to 6 p.m.).

(ii) *Main lines*

The main aim of the experiment was to compare three different selection strategies; selection in an Undivided population (treatment U), selection in each of 10 sublines which were reconstituted every 6th generation by Crossing after Culling the 5 lowest sublines (treatment CC), and selection in each of 10 sublines which were reconstituted every 6th generation by Crossing after Retaining all 10 sublines (treatment CR). There were two replicates (a and b) of each treatment. For each replicate of each treatment, 50 pairs of parents were selected from 250 male and 250 female progeny scored, giving a proportion selected of 20 %. The 10 highest pairs of unselected flies were assortatively mated during generations 0 to 16, and used as replacement matings where necessary.

For each replicate of treatment CC, five sublines were discarded prior to selecting the parents for generations 6, 12 and 17. These were the sublines of lowest mean bristle number, pooled over the two generations preceding that generation in which the sublines were crossed. In these three generations, twice as many flies were scored per surviving subline, in order to maintain the selection intensity of 20 %. Thus the CC lines went through three population bottlenecks each of 25 pairs.

In treatments CR and CC, the selected parents within each replicate were randomly mated at generations 6, 12 and 17, no regard being taken of sublines. In all other generations prior to generation 18, only random mating within sublines was allowed for these two treatments.

Each of the six lines (Ua and Ub, CRa and CRb, CCa and CCb) was initiated with 250 pairs of flies, derived equally from the one set of 50 full-sib families obtained from the base population.

The first generation of progeny from the foundation families contributed one full-sib group of five pairs from each family to each of the six initial selection lines. Selection in this initial generation, denoted zero (G. 0), operated only within these full-sib family groups. Commencing lines with one randomly selected

pair per foundation family would have increased the probability of some line(s) initially including a particular favourable gene, and other line(s) never including it. After G. 0, selection operated both within and between families, subject to any restraint imposed by the subline structure of the lines.

Three cycles of selection within lines followed by crossing among lines were conducted in the CR and CC lines, with the final cycle ending at G. 17. Although the main comparison of selection strategies thus finished at that time, selection was continued in the six main lines (Ua, Ub, CCa, CCb, CRa, CRb), in each case using mass selection of the top 50 out of 250 for each sex. Thus from G. 17 onwards, each of the six main lines was maintained as a large undivided population, in exactly the same way as Ua and Ub had been maintained since G. 0. Selection in all six main lines was continued by K.A.R. until G. 31, and subsequently by Dr B. Yoo who ceased selection in the various lines between G. 86 and G. 89. A detailed discussion of the long-term response to selection in each of the main lines is given elsewhere (Yoo, 1980*a*).

In having three cycles of subdivision followed by selection in an undivided population, the design of the experiment reported in this paper is intermediate between the single cycle and repeated cycle structures used by Madalena & Hill (1972) and Madalena & Robertson (1975).

(iii) *5-pair lines*

At G. 6 the ten sublines of CRa were maintained as separate entities, as well as being crossed to form the new set of CRa sublines. The separate set of 5-pair lines thus obtained was denoted S1 to S10, the numerals corresponding to the numbering of the CRa sublines. For these S lines, and all other lines split off from the six main lines, numbering of generations corresponded to that used for the main lines, i.e. the generation at which the S lines were named was denoted G. 6, not G. 0. At G. 9, five S lines were discarded leaving S5 and S9 (the two highest), S3 and S10 (the two lowest), and S8 (with an intermediate phenotype). S3 and S10 were discarded at G. 16. At G. 18, the two 5-pair lines that were then highest (S5 and S8) were crossed to produce S5 × 8, which was maintained as a 10-pair selection line. Selection was continued in S9 until G. 28, and in S5, S8 and S5 × 8 until G. 31.

(iv) *Lethal testing*

Between generations 12 and 16 the presence of recessive second and third chromosome lethals was tested in all 6 main selection lines, and in S5, S8 and S9, using a specially constructed tester stock marked by dominants (Cy; Ubx)/ ap^{Xa}, as described by Yoo (1980*b*). Thirty or more successive non-wild type flies were taken as sufficient evidence that a chromosome under test contained a lethal. All lethals detected were allelism-tested within each line to enable the frequency of particular lethals within each line to be estimated. Any lethal present more than once in any line was allelism-tested to all other such lethals in all other lines. In treatments CR and CC, an equal number of test matings was set up for each subline of each replicate.

3. RESULTS

(i) *The three strategies of selection*

(a) *Response during the three cycles of subdivision*

The results of selection until G. 17 in each replicate are shown for each selection strategy in Fig. 1. The generations at which crossing of sublines occurred are indicated by arrows. There is very close agreement between the two replicate lines of CR for the first 10 generations, and of U and CC for the first 12 generations. At G. 13, Ub and CCb fell somewhat behind Ua and CCa respectively. In sub-

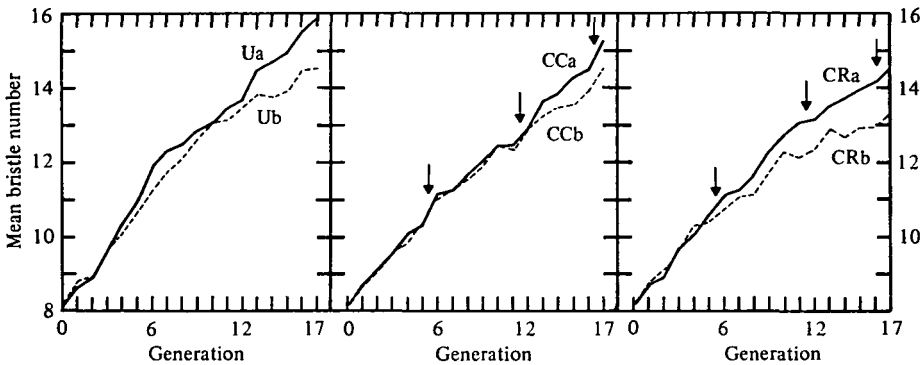

Fig. 1. Response to selection in each replicate for each selection strategy during the three cycles of subdivision. Arrows indicate the end of each cycle.

sequent generations, however, the rate of response in CCb was very similar to that in CCa. CRb fell behind CRa at around G. 10. Having fallen behind, both Ub and CRb subsequently showed a slightly slower rate of response.

Some light may be shed on the differences between replicates by the results of the lethal tests conducted in all lines between G. 14 and 16, summarized in Table 1. A total of 14 and 22 lethals were detected in the six lines on chromosomes 2 and 3 respectively. Of these, 10 and 16 respectively were detected on only one of the chromosomes sampled within a line, and were not allelism-tested to lethals in any other line. Instead, attention was focused on the 4 second chromosome and 6 third chromosome lethals that were detected more than once in any line. A complete allelism test among these 10 lethals indicated that in only one case was the same lethal detected in more than one line: it occurred with a frequency of 4 % in both Ub and CCb. The only lethal with an appreciable frequency was a second chromosome lethal in CCa, which was widely distributed among the CCa sublines, with an overall frequency of $0{\cdot}21 \pm 0{\cdot}06$ at G. 16. Because of its appreciable frequency, its effect on bristle number was subsequently estimated from a sample of 92 carriers at G. 22–23, and found to be about 0·6 bristles, or 0·4 phenotypic standard deviations. It is quite possible, therefore, that some of the difference between CCa and CCb in the final generations of the third cycle of subdivision could have been due to this allele.

Table 1. *Results of the lethal tests conducted in all 6 main selection lines*

			Chromosome 2			Chromosome 3		
Line	Generation at which lethal test was conducted	Number of flies from which one 2nd and one 3rd chromosome were sampled	Number of different lethals detected in each line	Frequency of each lethal: Occurring only once in a line	Frequency of each lethal: Occurring more than once in a line	Number of different lethals detected in each line	Frequency of each lethal: Occurring only once in a line	Frequency of each lethal: Occurring more than once in a line
Ua	14	44	1	0·02		3	0·02 0·02 0·02	
Ub	14	47	4	0·02 0·02 0·02	0·09	7	0·02 0·02 0·02 0·02 0·02 0·02	0·04*
CRa	15	46	3	0·02	0·09 0·07	5	0·02 0·02 0·02 0·02 0·02	
CRb	15	42	1	0·02		2	0·02	0·07
CCa	16	47	3	0·02 0·02	0·21	3	0·02	0·04 0·04
CCb	16	48	2	0·02 0·02		2		0·04*0·04
Totals			14	10	4	22	16	6

* Of those lethals that were detected on more than one chromosome within any line, this is the only case in which the same lethal was detected in different lines.

As the effect on bristle number of the other lethals was not estimated, it is not possible to attribute the difference between replicates to specific lethals in either treatments U and CR. However, the detection of so many different lethals during the last few generations implies that they may be at least in part responsible for the differences between replicates.

In order to provide a clearer comparison of the three selection strategies, selection response for each treatment was pooled over replicates. Using the data available at G. 17, average response in the three treatments U, CC and CR was estimated as $7{\cdot}03 \pm 0{\cdot}69$, $6{\cdot}74 \pm 0{\cdot}37$ and $5{\cdot}70 \pm 0{\cdot}59$ respectively, from which it is evident that there were no significant differences among treatment means. Despite this lack of significant differences, the relative performance of each treatment is of interest and is illustrated in Fig. 2. The most obvious result is the lack of superiority of the divided populations. By the time of the first crossing of lines, CR and CC had fallen behind U and remained inferior for all subsequent generations.

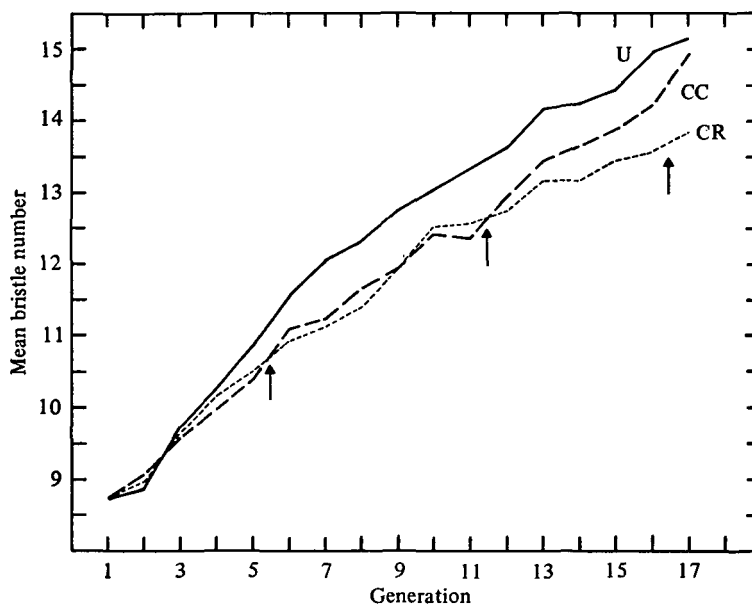

Fig. 2. Average response to selection for each selection strategy during the three cycles of subdivision. Arrows indicate the end of each cycle of subdivision.

The similarity of CR and CC during the first cycle of selection is not surprising, because it was not until after G. 5 that they were treated differently. Selection among sublines in treatment CC after generations 5, 11 and 16 produced relatively large changes in mean bristle number in comparison to treatment CR in which all sublines were retained. However, despite the effect of selection among sublines, CC did not become noticeably superior to CR until the third cycle of subdivision. The final selection between sublines changed CC's mean from midway between CR and U, to a level much closer to U. At G. 17, however, CC was

still lower than U. In summary, during three cycles of selection and crossing, subdivision of the population did not result in faster response to artificial directional selection.

Some insight into the nature of the difference between the three selection strategies can be obtained by examining the relative contribution of each of the 50 initial families to each selection line. For each generation during the three cycles of subdivision, Fig. 3 shows the variance of the percentage contribution

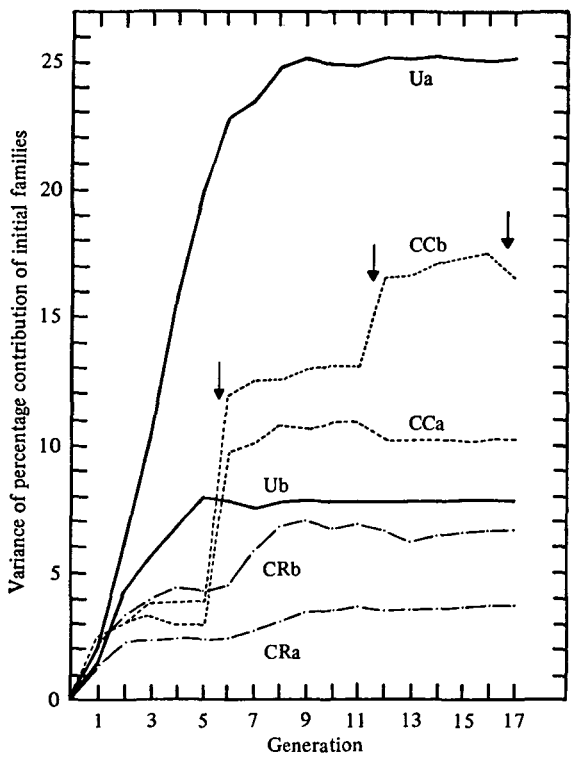

Fig. 3. Variance of percentage contribution of initial families to each of the six main lines throughout the three cycles of subdivision. Arrows indicate the end of each cycle.

of the 50 initial families to each selection line. During the first cycle of subdivision (generations 0 to 5), the variance of initial family contribution was greater in both undivided lines (Ua and Ub) than in any of the subdivided lines. This is to be expected, as the subline structure partly restricts 'competition' among families. The extraordinarily high variance of initial family contribution in Ua in subsequent generations is a consequence of one initial family becoming so predominant that by G. 17 it contributed 35% of all the genes in Ua. This represents almost twice the final contribution of any other family to any other line, and is thus an atypical result for the set of lines in this experiment. The variance of initial family contribution remained relatively low throughout the

three cycles of subdivision for CRa and CRb, indicating that the combination of old sublines and creation of new sublines between generations 5 and 6, 11 and 12, and 16 and 17, did not in itself increase the potential for selection between initial families. Only when the creation of new sublines was preceded by selection among lines (as in CCa and CCb) did selection among initial families occur, with a consequent increase in variance of initial family contribution. The first selection among sublines (between generations 5 and 6) substantially increased the variance of initial family contribution in both CCa and CCb. The second selection among sublines (between generations 11 and 12) further increased the variance of initial family contribution in CCb but not in CCa, and the final selection among sublines had no effect in either line.

Further information on selection among initial families can be obtained by observing the elimination of initial families in successive generations. For each main selection line, Table 2 shows the number of families still represented at each generation up to the end of the third cycle of subdivision. It is evident from Table 2 that the number of initial families eliminated during the first five generations was similar in all six main lines. By G. 5, the average number of

Table 2. *Number of initial families contributing to each of the six main lines during the three cycles of subdivision*

	Main line					
Generation	Ua	Ub	CRa	CRb	CCa	CCb
0	50	50	50	50	50	50
1	43	46	43	39	42	43
2	39	41	42	37	40	41
3	37	41	42	35	39	37
4	36	41	40	35	37	37
5	33	40	40	35	37	37
6 to 17	33	40	40	35	19	18

families remaining from the 50 initial families was 37. No more families were eliminated after G. 5 in Ua, Ub, CRa and CRb. However, as soon as selection among sublines occurred (in CCa and CCb between generations 5 and 6), a further 18 families in CCa and 19 families in CCb were eliminated, leaving a remainder of 19 and 18 respectively. The second and third cycle of selection among sublines did not result in the elimination of further initial families.

In addition to knowing how many initial families were eliminated, it is important to know the extent to which the same initial families were eliminated from or made substantial contributions to each main line. In general, the pedigree analysis conducted on the six main lines indicated that no single initial family made a substantial contribution to all or even to most of the main lines. Indeed, in five of the six main lines at G. 17, the highest percentage contribution came from five different initial families. Only in one case did the same initial family have the highest contribution to more than one line: initial family number 49 had final

contributions of 15·1 % to Ub and 14·9 % to CRb. However this family's contribution to the other four main lines was either relatively low (3·1 % to CRa and 1·7 % to CCb) or zero (Ua and CCa). The tendency of one family to have a high contribution to one main line but very low or zero contributions to other lines is indicated in Table 3. It can be seen that none of the initial families with the

Table 3. *Percentage contributions to each main line at generation 17, of the five initial families having the highest contributions to one of the main lines at generation 17*

Initial family identification number	Percentage contribution at generation 17					
	Ua	Ub	CRa	CRb	CCa	CCb
17	35·0*	7·2	2·1	0·5	5·0	0·0
19	5·4	1·7	3·8	2·6	14·7*	0·0
23	1·8	0·8	4·6	1·1	0·0	18·7*
39	0·8	1·2	9·7*	0·0	5·6	0·0
49	0·0	15·1*	3·1	14·9*	0·0	1·7

* Highest percentage contribution to each main line at generation 17.

highest final contribution to one main line was represented in all six main lines at G. 17: two of the families were represented in only four main lines, and the other three were represented in five main lines. In fact, although not shown in Table 3, only one of the 50 initial families was still represented in all six main lines at G. 17, and the maximum final contribution of that family to any of the main lines was only 5·0 %. On the other hand, only three of the 50 initial families were eliminated from all main lines by G. 17. Thus nearly all initial families made lasting contributions to at least some lines, and no single initial family made a substantial contribution to most or all of the main lines.

It was seen in Table 2 that the first selection among sublines in CCa and CCb resulted in a substantial reduction in the number of initial families still represented. Of the 19 and 18 initial families still contributing to CCa and CCb respectively between generations 6 and 17, only 4 families were common to both lines; 15 of the families in CCa were not represented in CCb, and 14 of the families in CCb were not present in CCa. Thus even the strong selection among initial families in the two CC lines resulted in two very different sets of family contributions.

(ii) *5-pair lines versus 50-pair lines*

The response in various 5-pair lines is compared with the average response in the two undivided 50-pair lines in Fig. 4. The undivided 50-pair lines showed continual and almost linear response to selection throughout the 31 generations shown in Fig. 4. Indeed, throughout most of this time, these lines showed very close agreement with the simple linear prediction of $ih^2\sigma_P$ (= 0·44 bristles) per generation, obtained from the base population parameter estimates. In reaching an average phenotype of $20{\cdot}6 \pm 0{\cdot}08$ bristles at G. 31, they were thus very

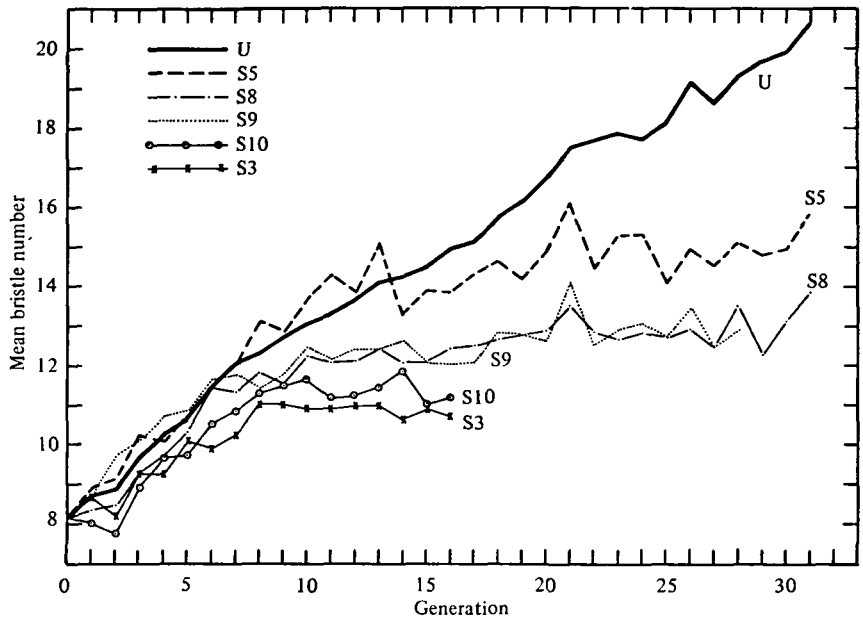

Fig. 4. Average response to selection in the undivided 50-pair lines (U) compared with response to selection in various 5-pair lines (S).

close to the value of 21·8 predicted from the base population estimates of h^2 and σ_P.

For 5-pair lines, however, the picture is completely different. Those that were lowest at G. 9 (S3 and S10) were always inferior to the 50-pair lines, and, failing to show any response beyond G. 9, were discarded at G. 16, at which stage their total response was approximately one half that of the 50-pair lines. Of the three remaining 5-pair lines, S5 and S9 were both initially better, and S8 was initially worse than the 50-pair lines, until around G. 6, when all three 5-pair lines were similar to the 50-pair lines. During this phase, the greatest superiority over the mean of the 50-pair lines was shown by S9 at G. 2 (a superiority of $0{\cdot}81 \pm 0{\cdot}24$ bristles), and by S5 at G. 3 (a superiority of $0{\cdot}52 \pm 0{\cdot}26$ bristles). Beyond G. 6, S8 and S9 showed very similar response, falling behind the 50-pair lines, and soon plateauing at around 13 bristles, thus giving, beyond G. 25, a total response of less than one half that of the 50-pair lines. Line S5 on the other hand, showed a second phase of superiority over the 50-pair lines until G. 14, but it also soon reached a plateau.

The lethal analysis conducted on S5, S8 and S9 at G. 12 detected no lethals with an appreciable frequency on either chromosome 2 or 3. Thus the difference between S5 and the other two lines cannot be attributed to lethals.

The selection line established from a cross between S5 and S8 at G. 18 does, however. provide some indication of the nature of the superiority of S5. Fig. 5 indicates that S5 × 8 started with a phenotype not signicantly different from the mid-parent value of S5 and S8, and showed a gradual response until it reached

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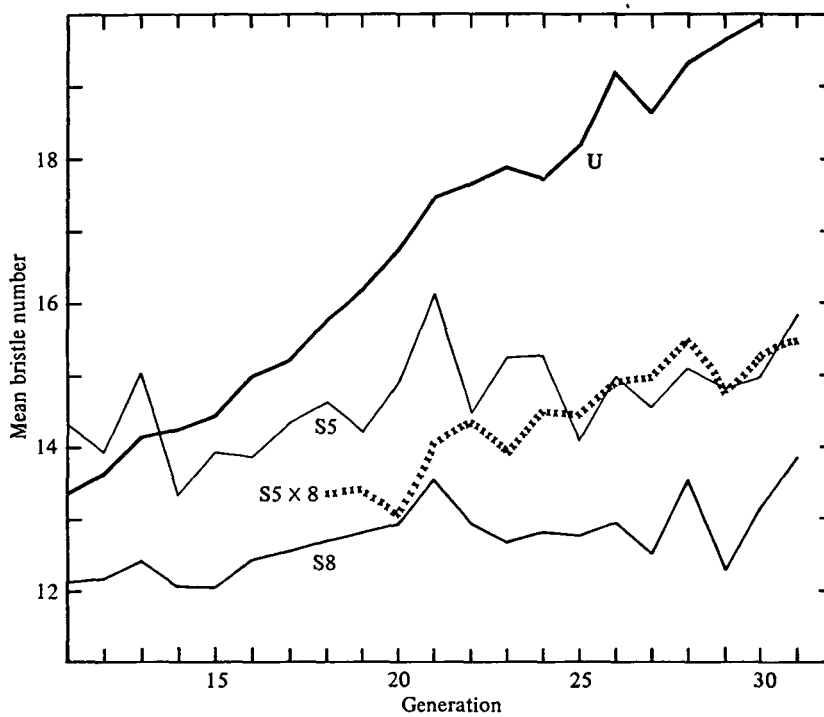

Fig. 5. Response to selection in the 5-pair lines S5 and S8 compared with the cross between them, S5 × 8, and compared with average response in the undivided 50-pair lines, U.

the same level as its higher parent, S5, after which it also appeared to have plateaued. This behaviour is compatible with the superiority of S5 being due to several additive alleles, fixed in S5 and lost from S8. It is not compatible with the difference being due to one allele of large additive effect, because in this case initial response in S5 × 8 would have been much more rapid.

4. DISCUSSION

(i) *The three strategies of selection*

It is evident from the results that subdivision of the population did not result in a faster response to artificial directional selection for abdominal bristles in *Drosophila melanogaster* in the short term. These results agree with those of all previous similar experiments with which they can be directly compared. The difference between the results of the experiment by Katz & Young (1975) and all other experiments on sublining, including the present one, is most likely a consequence of the former's difference in aims and design.

How well do our results correspond to those predicted by Madalena & Hill (1972) for an entirely additive model? Briefly, their predictions were (i) that lines in which there is repeated subdivision with no between-line selection (lines

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CR in this experiment) will reach the same limit as undivided lines of the same total size (lines U), but at a much slower rate, and (ii) that repeated subdivision with between-line selection at the intensity used here (5/10 in the CC lines) would most likely produce an inferior response in the early generations, and would certainly result in a lower limit when compared with an undivided population. In addition, their simulation results (see, for example, their Fig. 5) clearly indicated that during the course of our experiment, the CR lines should show a slower response than the CC lines.

Bearing in mind that none of the differences were significant, it was seen that repeated subdivision with no between-line selection (CR lines) did produce a slower rate of response, as did repeated subdivision with between-line selection at an intensity of 5/10 (CC lines). And at least by the end of our comparison of lines, CR was inferior to CC. Thus, our results are in agreement with predictions based on a model in which artificial directional selection for abdominal bristle number in *Drosophila melanogaster* results in entirely additive gene action for overall fitness.

Experiments of the type reported here are sometimes interpreted in the light of Wright's shifting balance theory of evolution (reviewed by Wright (1977*b*), chapter 13) which in the present context predicts that sublining will be advantageous, but only in the presence of a 'large number of selective peaks', or in other words, multiple-peak epistasis. As carefully explained by Wright in the same chapter, multiple-peak epistasis is most likely to arise with a quantitative character having 'the optimum not far from the mean', i.e. for a quantitative character undergoing stabilizing selection. If there is no epistasis, then Wright's shifting balance theory does not apply and hence cannot be tested. Thus the failure of sublining to achieve a faster response in this and other similar experiments could be due to Wright's theory being incorrect, or to the lack of epistasis, or to a combination of both these reasons. The close agreement between the results obtained here and the predictions arising from an entirely additive model (as described above) indicates that a sufficient explanation for the observed results is a lack of epistasis. Thus our results provide no direct evidence for or against Wright's shifting balance theory. Indeed, direct evidence on Wright's shifting balance theory can only be obtained from selection programmes in which epistasis is certain to be present.

Wright has always believed (as reviewed in 1977*b*, Chapter 13) that 'if each gene substitution were favourable or unfavourable in itself' (i.e. if there is no epistasis) then there is no advantage to be gained from sublining. Why then did Wright and Lush recommend sublining in artificial directional selection programmes? They did so because they believed (1) that Wright's shifting balance theory is correct, (2) that artificial directional selection amounts to selection for 'anatomical or physiological intermediates' (Lush, 1937, Chapter XI), (3) that 'nearly all genes. . . are epistatic in their effects' (Lush, 1937, Chapter XXXVIII).

We have already seen that our results shed no light on the first assumption. They do, however, indicate that the latter two assumptions do not hold sufficiently

to affect the outcome of artificial directional selection for abdominal bristle number in *Drosophila melanogaster*.

(ii) *5-pair lines versus 50-pair lines*

While illustrating the futility of expecting continual response if effective population size is small, the behaviour of the 5-pair lines also corresponds to some extent with the relevant theory of Baker & Curnow (1969) and Madalena & Hill (1972), who predicted that the best of the small lines could be superior to a large line for a short time during the very early stages of a selection programme. Indeed, calculations have shown that the behaviour of S9, the best of the 5-pair lines in the short term, corresponds quite well to the quantitative predictions arising from an additive model, as derived by Robertson and published by Madalena & Hill (1972).

The general conclusion to be drawn from the comparison of response to selection in 50-pair versus 5-pair lines is quite clear. With a relatively large effective population size (in this case, slightly less than 100), response to directional artificial selection for at least 30 generations corresponded very closely with that predicted from the base population, using the classic prediction formula $ih^2\sigma_P$. Although the best of the 5-pair lines exceeded the 50-pair lines in the early generations, average response to directional selection in 5-pair lines soon fell behind that predicted from $ih^2\sigma_P$, and soon reached a plateau.

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