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Long-term selection for a quantitative character in large replicate populations of *Drosophila melanogaster*

1. Response to selection

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SUMMARY

The response to long-term selection for increased abdominal bristle number was studied in six replicate lines of *Drosophila melanogaster* derived from the *sc* Canberra outbred strain. Each line was continued for 86–89 generations with 50 pairs of parents selected at an intensity of 20%, and subsequently for 32–35 generations without selection. Response continued for at least 75 generations and average total response was in excess of 36 additive genetic standard deviations of the base population (σ_A) or 51 times the response in the first generation. The pattern of long-term response was diverse and unpredictable typically with one or more accelerated responses in later generations. At termination of the selection, most of the replicate lines were extremely unstable with high phenotypic variability, and lost much of their genetic gains rapidly upon relaxation of selection.

The variation in response among replicates rose in the early phase of selection to level off at approximately 7·6 σ_A^2 around generation 25. As some lines plateaued, it increased further to a level higher than would be accommodated by most genetic models. The replicate variation was even higher after many generations of relaxed selection. The genetic diversity among replicates, as revealed in total response, the individuality of response patterns and variation of the sex-dimorphism ratio, suggests that abdominal bristle number is influenced potentially by a large number of genes, but a smaller subset of them was responsible for selection response in any one line.

1. INTRODUCTION

Effective population size has been recognized as one of the most important factors determining the consequences of artificial selection, especially long-term responses and selection limits (Robertson, 1960, 1970; Hill & Robertson, 1966; Jones, Frankham & Barker, 1968; Eisen, 1975; Ruano, Orozco & López-Fanjul, 1975). It should be reasonably large when quantitative aspects of long-term selection are the primary concern, as in the case of animal breeding, because the be-

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haviour of a small selection line is likely to be dominated by genetic drift which causes loss of genetic variability not only for the character under consideration but for the whole genetic complement. However, current selection theory does not provide adequate predictions about long-term results of selection in large populations (Robertson, 1966; Kempthorne, 1977), in spite of the development of finite population theory in the past two decades (Kimura, 1957; Robertson, 1960, 1970; Hill & Robertson, 1966; Latter & Novitski, 1969). So, many facets of long-term selection have had to be discovered through experimentation, mostly with laboratory animals and poultry (Falconer, 1960; Al-Murrani, 1974).

Although a considerable number of selection experiments have been carried out for this purpose, it has been realized only recently that the result of a single selection line is disappointingly unreliable and thus proper replication is mandatory in any selection experiments (Hill, 1972; Falconer, 1973; Kempthorne, 1977). This is particularly so in long-term selection experiments where results are largely unpredictable and agreement among replicates is often poor (e.g. Clayton & Robertson, 1957). Also the replicate variation of long-term response has been shown to be valuable in understanding the genetic nature of the base population and of selection progress (Robertson, 1960, 1970; Latter, 1969).

In an experiment to evaluate Robertson's (1960) theory of selection limits (Jones *et al.* 1968), it was suggested that the poor agreement among replicates might be due to genes of large effect initially at low frequencies and that replicate variation might be reduced by using a larger population size. However, in their experiment replication was very limited for the larger populations, and further experimentation was needed to confirm their suggestion.

The object of the present study was to investigate the long-term behaviour of large replicate lines (50 pairs of parents) selected for increased abdominal bristle number, with respect to the pattern, duration and total amount of response. Various analyses were carried out to better understand the underlying causes of their behaviour. The results indicated that response continued for the full duration of selection (86–89 generations) in some lines, but showed large variation among replicates, and that accelerated response, though unpredictable, was a common feature of the response pattern.

2. MATERIALS AND METHODS

The selection lines were originally established in another experiment (Rathie & Nicholas, 1980). The base was a large cage population of the *sc* Canberra strain of *Drosophila melanogaster*, derived from the Canberra strain (Sheridan *et al.* 1968) by introducing *sc* (scute) and y^2 (yellow body) through repeated backcrossing to make bristle scoring easier and to provide a check against contamination (Rathie, 1969). An egg sample from the cage was cultured to get virgin flies, which were mated in single pairs to obtain 50 full-sib families. Six lines were started each with 250 males and 250 females taken equally from the same 50 families, and so any

specific autosomal gene must have been sampled in all the six lines with probability of 0·98.

In each generation 50 individuals were selected out of 250 scored within each sex except when culling of sublines was necessary (see below). Selection was for increased number of bristles on one abdominal sternite, the fourth in males and the fifth in females. The genetic correlation between the two sternites has been shown to be unity within sexes (Hammond, 1973; Yoo, 1974*a*).

Three different population structures were imposed in the first 17 generations: Ua and Ub (*U*ndivided, replicates *a* and *b*) were selected in single large lines; CRa and CRb (*C*rossing with *R*etention) were each selected within 10 sublines of equal size which were crossed and derived afresh from the cross every 6th generation; CCa and CCb (*C*rossing with *C*ulling) were also sublined but the 5 lowest sublines were culled before crossing. These original designations are kept in this paper for cross reference to Rathie & Nicholas (1980).

The 6 selection lines have been regarded as replicates in the present experiment. This was possible as: (1) the effects of the population structure on response to generation (G) 17 were rather small relative to the variation between replicates; (2) it has been shown for additive genes that the expected selection limit would not be affected by sublining when effective population size and selection intensity were kept constant (Robertson, 1960), and this prediction was largely verified in a similar experiment using sternopleural bristle number (Madalena & Robertson, 1975).

From G 18, all the lines were maintained as single large lines each with 50 pairs of parents selected out of 250 pairs scored until G 86 in Ua and CCa, G 87 in Ub and CRa and G89 in CRb and CCb. These lines were then continued until G 121 with 50 pairs of parents taken at random in each generation; 100 pairs were scored in the first 7 generations and at intervals of 3–5 generations thereafter except in G 115–117, when 250 pairs were scored.

Parents were randomized equally among 5 cream jars (142 ml) and selection was on a within-jar basis, except for the following generations: in the first 17 generations and for brief periods of 9 generations in some lines, viz. G 57–65 for CRa and CCa and G 68–76 for Ua and Ub, single-pair matings were set up in $2{\cdot}5 \times 7{\cdot}6$ cm vials, and selection was within lines or sublines without regard to culture of origin. The two different culture methods were found to have negligible environmental effects on abdominal bristle number. Parents were allowed to lay eggs for 3–4 days, depending on fecundity, and all flies were raised on a dead yeast-fortified medium (Medium F of Claringbold & Barker, 1961) at $25 \pm 0{\cdot}5$ °C and 65–70% relative humidity.

3. RESULTS

(i) *The base population*

The phenotypic parameter estimates in a large sample scored in the first generation (Rathie, 1976) are summarized in Table 1. As compared with the corresponding wild-type population (Sheridan *et al.* 1968), the *sc* population was much

lower in mean bristle number due to the substitution of *sc* for sc^+. It has been suggested that this substitution effect was on the average additive in the present selection lines (Yoo, 1974*b*). The g_1 and g_2 values were similar to those estimated in another sample taken later from the same cage population (Hammond & James, 1970). Both studies indicate that the distribution is skewed upwards, probably more in males than in females, and tends to be leptokurtic.

Table 1. *Phenotypic and genetic parameters of the base population*

Statistics	Males	Females
Mean*	6·95	9·35
Phenotypic standard deviation*	1·44	1·73
Skewness (g_1)*	0·333 ± 0·070	0·136 ± 0·070
Kurtosis (g_2)*	0·239 ± 0·140	0·234 ± 0·140
Additive genetic components†:		
Autosomal	0·173 ± 0·018	
Sex-linked	0·026 ± 0·016	
Heritability	0·199 ± 0·024	
Additive genetic standard deviation	0·641	0·772

* From Rathie (1976). † From Hammond (1973).

The autosomal and sex-linked additive genetic components (Table 1), as proportions of phenotypic variance, were estimated in a large-scale partitioning of phenotypic variance and covariance (Hammond, 1973). These estimates were added to get a heritability of 0·199, assuming a complete dosage compensation for sex-linked genes affecting abdominal bristle number as shown by Frankham (1977).

(ii) *Response patterns*

Female mean bristle numbers in each generation are shown in Fig. 1, including the first 30 generations from Rathie (1976). In general, the genetic gain per generation remained unexpectedly high until around G 76, when Ua, Ub and CRa abruptly stopped responding to selection. When selection ceased, CRb and CCb were still showing substantial progress. It appeared uncertain by G 86 whether CCa had plateaued, but subsequent selection in another laboratory confirmed a continuous, though slow, response (Dr B. L. Sheldon, pers. comm.).

The selection lines tended to maintain a definite order for many generations, which was occasionally disturbed by accelerated responses in some lines. The response pattern was quite characteristic of each line with few common features apart from there being accelerated responses in all but one line (Ua). The peak of CCb at G 59 was caused by an apparent reversion of *sc*, which also affected the phenotypic standard deviation (Fig. 4). This reversion was eliminated immediately after its occurrence. Individual patterns may be summarized as follows:

Ua: Steady and continuous response. Highest to G 20, but lowest at the plateau.

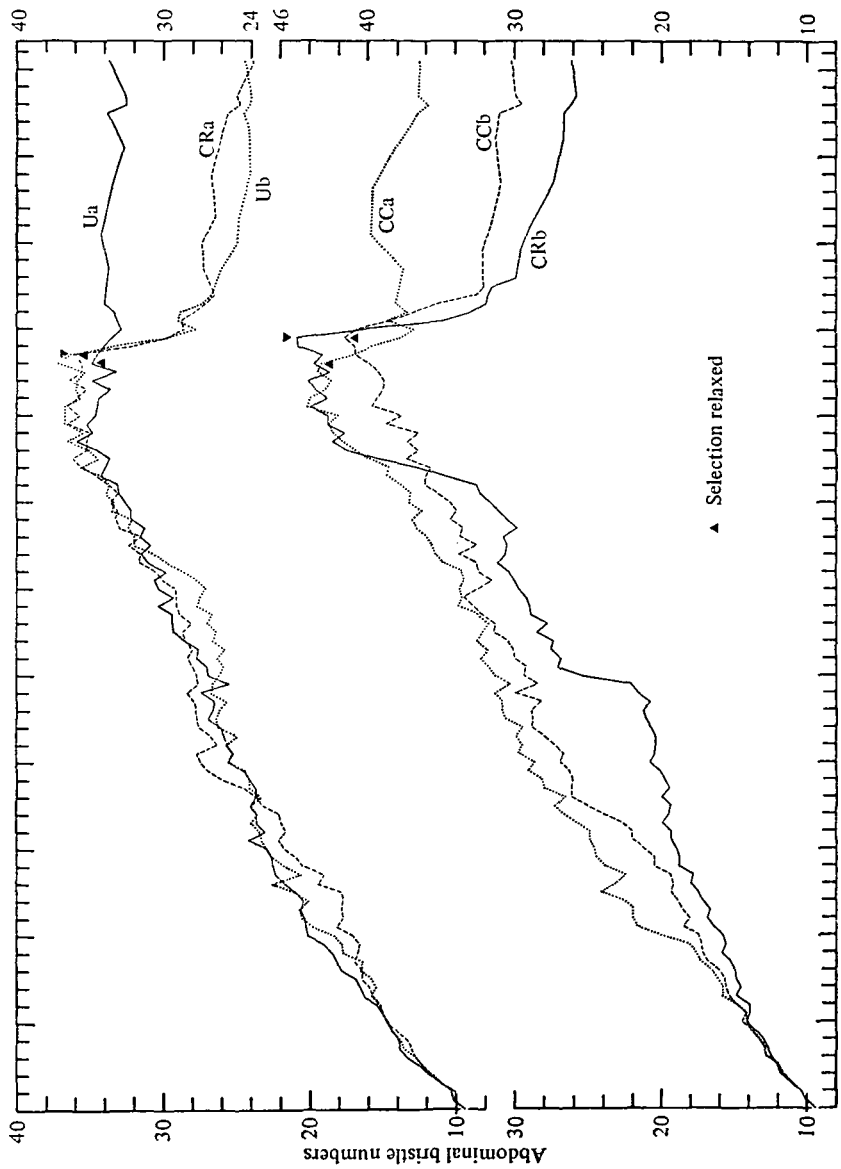

Fig. 1. Female mean bristle numbers plotted against generations.

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Ub: Accelerated responses around G 20 and 62 with an intervening period of cessation (G 44–53). Plateaued.

CRa: Curvilinear response before 2 successive accelerations around G 28 and 37. Two further waves of response between G 60 and the final plateau.

CRb: Extraordinary. Increasingly lagged behind until a big, very rapid jump around G 50. Cessation around G 66 followed by another bigger jump around G 74. Finally the highest.

CCa: Highest until G 75 after the first acceleration around G 20. Step-wise responses around G 57 and 65. Acceleration around G 76 before the last slow-down.

CCb: Almost linear except for one acceleration around G 34.

The behaviour under relaxed selection was more consistent in that all but one line (Ua) declined very rapidly for the first few generations and then slowly approached a stable level. The final level had no apparent relation with the mean bristle number before selection was relaxed. Ua, which had previously shown no accelerated response, was very stable under relaxed selection with only a small decrease in mean even after 35 generations. Also, it may be noted that variability among the lines was much higher under relaxed selection than during selection.

(iii) *Sex-dimorphism ratios*

Fig. 2 shows the ratio of male to female mean bristle number, i.e. sex-dimorphism ratios; successive 5-generation averages were plotted against generations. This indicates that the amount of response in males relative to that in females was quite variable among different lines, although the response pattern was very similar between the sexes within a line. The final variability of the ratio among the lines was remarkable, ranging approximately from 0·64 in Ua to 0·81 in CRa, but it appeared to be a random scatter around the base value of 0·74, as might be expected in the absence of any deliberate selection for the ratio. There was no discernible relationship between the sex-dimorphism ratio and the selection response in females depicted in Fig. 1. Relaxed selection sharply increased the ratio in Ub and CRa presumably by eliminating some deleterious genes which had proportionately bigger effects in females.

(iv) *Total responses and their time scales*

Table 2 summarizes total responses, time scales and accumulative selection differentials, averaged over the sexes. In Ua, Ub and CRa, total response was estimated from the average of generation means after plateaux, while in the other 3 lines which were still responding at the end of selection, it was calculated from the mean in the last generation of selection. The total response and time scale in the latter should be taken as minimum estimates. Selection differentials were accumulated over the whole period of selection. In the table, the total response is expressed in four different ways: in bristle number units, in terms of phenotypic standard deviation (σ_P) and of additive genetic standard deviation (σ_A) in the base popula-

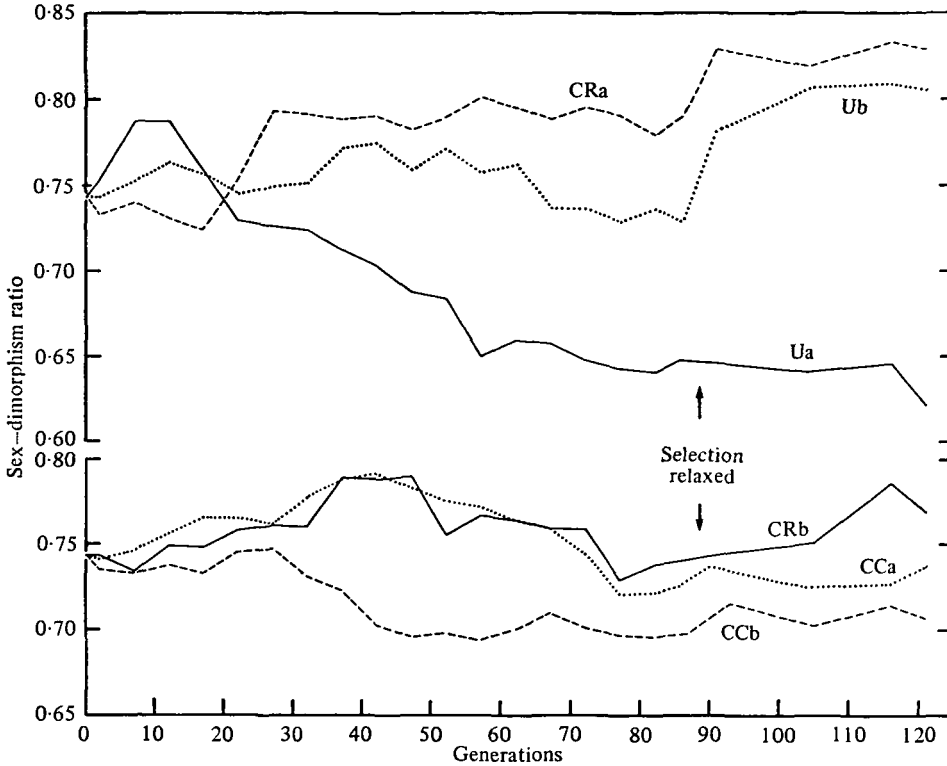

Fig. 2. The ratio of male to female means (sex dimorphism ratio). Successive 5-generation averages were plotted against generations.

Table 2. *The duration, half-life and total amount of response and cumulative selection differentials (sexes averaged)*

Line	Duration (gen.)	Half-life (gen.)	Total response*				Cumulative sel. diff.
			Bristles	σ_P	σ_A	ΔG_1	
Ua	76	24·0	20·2	12·6	28·2	39·9	270·2
Ub	77	29·5	23·2	14·6	32·6	46·4	349·2
CRa	75	34·0	23·8	15·0	33·6	47·8	374·4
CRb	89	52·0	30·7	19·3	43·2	61·4	339·9
CCa	86	32·5	29·1	18·2	40·9	58·1	383·8
CCb	89	36·0	27·3	17·1	38·4	54·5	358·0
Mean	82	34·7	25·7	16·1	36·2	51·3	345·9

* The total response is expressed in terms of bristle number, phenotypic (σ_P) and additive genetic (σ_A) standard deviations of base population and the response in the first generation (ΔG_1).

tion, and in multiples of the response in the 'first' generation (ΔG_1). The value of ΔG_1 was estimated from the regression of mean bristle number on generation (for the first 6 generations) pooled over the lines within sexes.

On the average, the response continued for at least 82 generations with a total response in excess of 16 σ_P, 36 σ_A, or 51 ΔG_1; the mean bristle number was in-

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creased from 8·15 to 33·88, an increase of 316%; and the 'half-life', i.e. the time taken to get one half of the total response, was 34·7 generations. The total response varied from 20·2 to 30·7 bristles, with the lowest being only 65% of the highest. It is noteworthy that the 3 lines which made the most genetic progress were those still responding at the last stage of selection. This means that if all the lines had plateaued, the replicate variation of total response and of time scale would have been higher.

Cumulative selection differentials, apart from the differing numbers of generations of selection, are as variable as the total response, being generally greater in those lines showing more total response. This is simply a reflection of the difference in phenotypic variance between the lines, as selection intensity was almost constant over generations and lines. On the surface, the total response appears to have been largely determined by the amount of selection applied in absolute terms, but it will become clear that there is no cause-effect relation between them.

(v) *Variation among lines in response*

The variance among lines of female mean bristle numbers is plotted against generations in Fig. 3. The variance was calculated on both the arithmetic and logarithmic scales; the means on the latter scale were estimated from the original mean and coefficient of variation using the formulae given by Wright (1952). In view of the extraordinary response pattern of CRb, the variance was in each case calculated for 5 lines only excluding CRb, as well as for all 6 lines.

Although the variance changed irregularly over generations, we still can visualize a curve which rises more or less like a sigmoid curve in early generations, approaching a *plateau* where it stays until G 50, and then steadily declines to reach a *trough* at G 74 before the *last peak*. This was possible by regarding the peaks around G 25, 43, 59 and 67 primarily as attributes of single lines, viz. the rapid response in CCa, and the lags in CRb, Ub and CRb respectively. The last peak should be taken as a minimum estimate of the variance at the limit, because the 3 highest lines had not stopped responding. The variances at the underlined levels are summarized in Table 3, including that estimated in G 115–117, i.e. after 26–31 generations of *relaxed* selection.

(vi) *The phenotypic variability and distribution of bristle numbers*

The phenotypic variability is expressed in terms of standard deviation in females (Fig. 4). The phenotypic standard deviation essentially remained stable at around 1·9 in all lines until G 14, after a slight initial increase from the base value of 1·73 perhaps as a result of adaptation to changes in environment. In this period, the mean was increased from 9·4 to 15·6, consequently resulting in a rapid and almost linear decrease in coefficient of variation from 18·5% to 12·1%. Thereafter, however, the phenotypic standard deviation rose in one line after another and finally reached a level around 5 bristles, except in Ua. The pattern of change was in general closely related to the selection response (Fig. 1). In particular, a large increase occurred almost always concurrently with an accelerated response. The

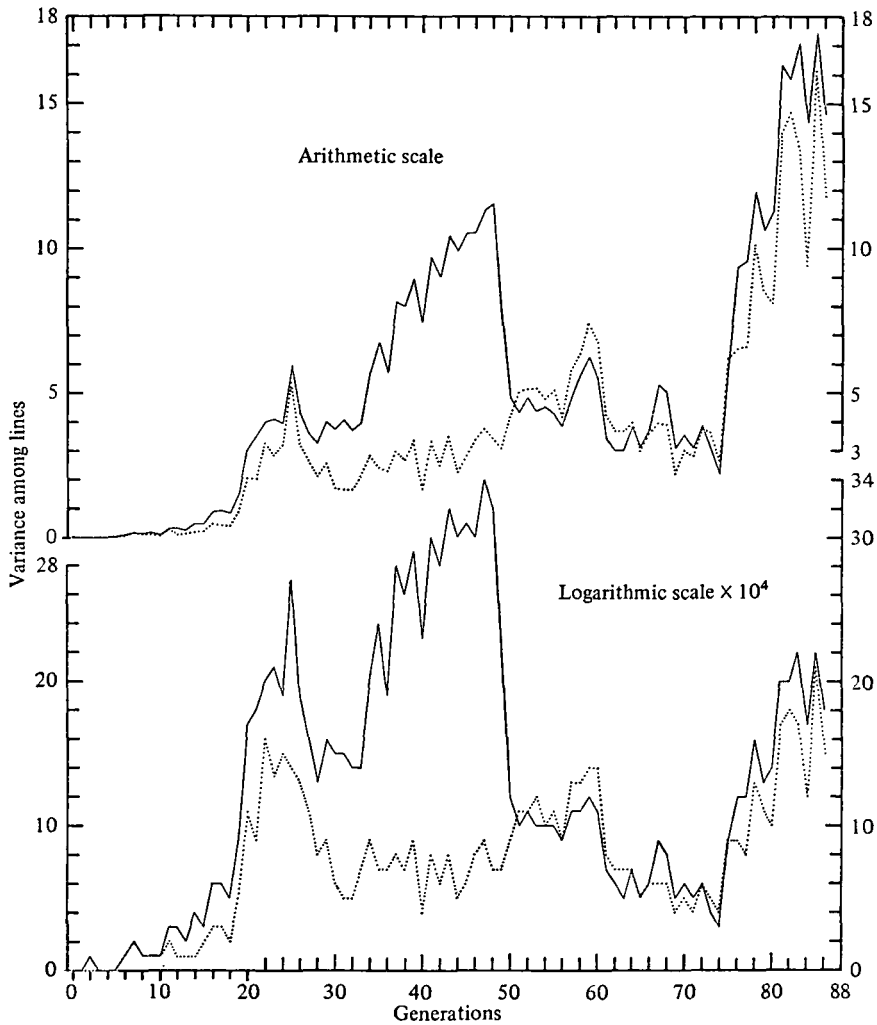

Fig. 3. The variance of female mean bristle numbers among the six replicate lines (continuous line) or among the five lines excluding CRb (dotted line).

Table 3. *The variance among replicates of female mean bristle numbers*

	Arithmetic scale		Logarithmic scale	
Levels*	In absolute units	In base σ^2_A units	In absolute units	In base σ^2_A units†
Plateau	4·5	7·6	0·0010	0·76
Trough	3·5	5·9	0·0005	0·39
Last peak	16·0	27·0	0·0020	1·57
Relaxed	23·2	38·9	0·0057	4·53

* Described in the text.

† The additive genetic variance on the logarithmic scale was calculated on the assumption that the heritability in the base population was the same on the two scales.

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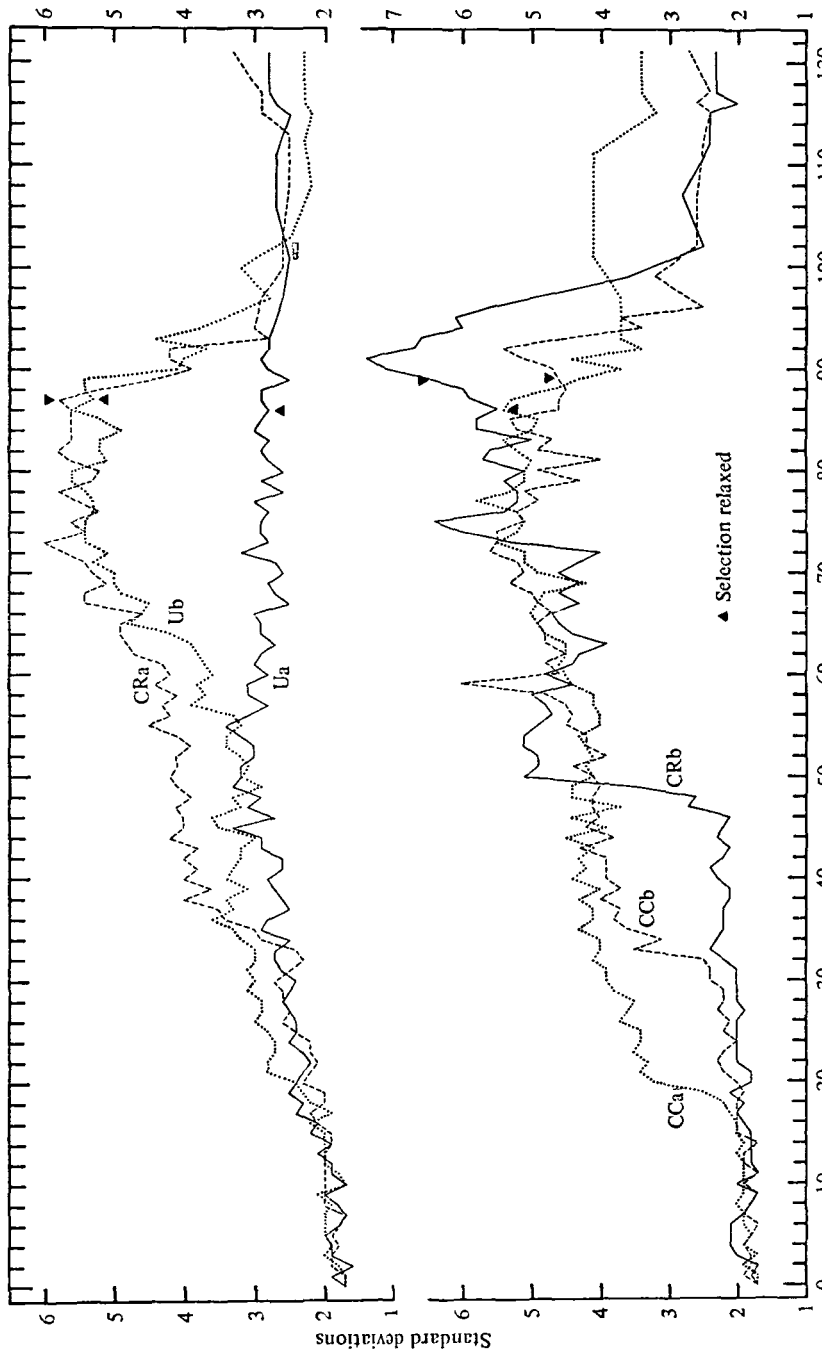

Fig. 4. Phenotypic standard deviations in females.

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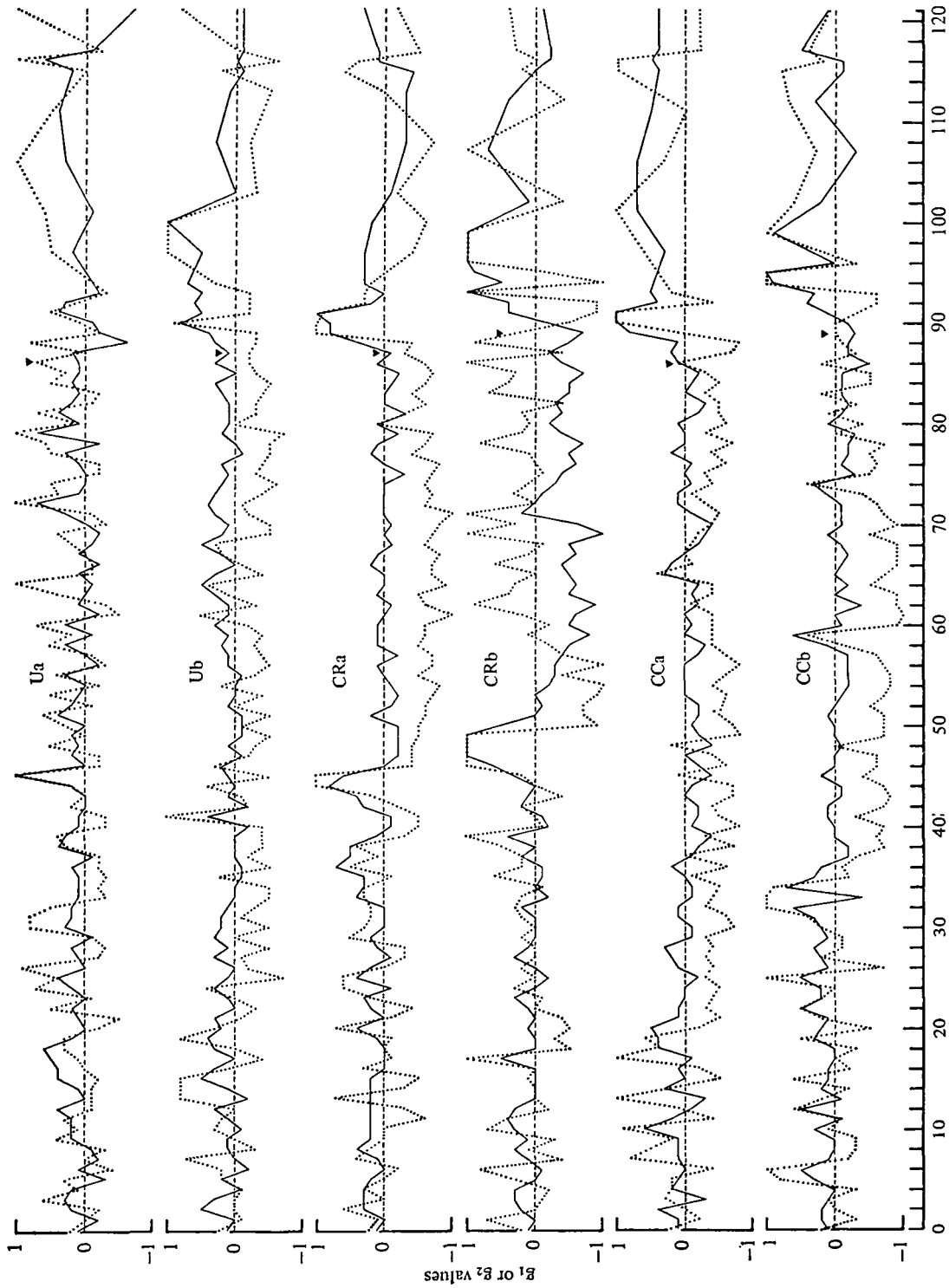

Fig. 5. g_1 (continuous line) and g_2 (dotted line) values plotted against generations; extreme values have been truncated at ±1.

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phenotypic standard deviation, once increased, seldom declined much until selection was relaxed. In Ua, the phenotypic standard deviation showed steady and slow changes to stabilize at the final level of about 2·8 bristles.

When selection pressure was removed, the phenotypic standard deviation rapidly declined, immediately or after a temporary increase for a few generations, except in Ua which showed very little change. After some 30 generations, the phenotypic standard deviation was considerably higher in CCa than in the other 5 lines which levelled around 2·5. It tended to increase again in CRa, where the mean was still declining at G 121, after reaching a low level at G 113. The phenotypic variability in males was generally lower, but patterns of change were very similar to those in females.

The skewness and kurtosis of the distribution of bristle numbers were measured by g_1 and g_2 statistics. Fig. 5 shows these statistics plotted against generations; as some values are extremely large or small, they have been truncated at ± 1. The distribution in the base population tended to be skewed upwards and leptokurtic (Table 1). This tendency persisted in early generations of selection. Subsequently, however, the distribution changed often in conjunction with accelerated responses and with concurrent increases in standard deviation. In particular, the original skewness tended to disappear or became reversed, and the distribution either became normal or bimodal in different lines. In Ua, selection had little influence on the distribution as might be expected from the response pattern.

When selection was relaxed, the distribution first became skewed upwards except in Ua, and platykurtosis, if present, disappeared; and then it returned to a state similar to that in early generations.

4. DISCUSSION

(i) *The total response and time scale of selection progress*

Robertson (1960) has shown that the total response is expected to be $2N_e \Delta G_1$, for low values of $N_e i$ and additive genes, with the half-life of selection progress being no more than 1·4 N_e generations, where N_e denotes the effective population size and i the standardized selection differential. In the present experiment, total response was on average $51{\cdot}3\Delta G_1$ with a half-life of 34·7 generations. As some lines were not at the limit, these should be under-estimates. However, even if selection had been continued further, the total response was unlikely to be greater than $N_e \Delta G_1$, assuming N_e to be about 60. This value of N_e has been approximated from the results of Buri (1956) and Nozawa (1970), taking into consideration the inbreeding effect of selection (Robertson, 1961). The failure of the response prediction should not be too surprising, given the high value of $N_e i$ (84).

The half-life of response appears to have been well below N_e generations, perhaps suggesting that most of the desirable alleles have been fixed (Robertson, 1960). On the other hand, according to a simulation study with multiple alleles (Latter & Novitski, 1969), the observed total response was only 55 % of the effective upper limit, although the observed half-life was close to the expected (37 generations).

These values were obtained from their equations (14) and (17) describing empirical relations of total response and half-life, respectively, with $N_e ig$, where g^2 measures the relative contribution of a locus to the total variance. It may be noted that the observed total response and half-life might have been inflated by the scale effect, which became apparent at later stages of selection.

Empirically, the total response and duration of response are well beyond the range of observed values summarized by Falconer (1960), after a review of 4 experiments with mice and *Drosophila*. Similar large and long-continued responses also were obtained in more recent experiments with large population sizes (Jones *et al.* 1968; Comstock, 1973; Enfield, 1977).

(ii) *The pattern of selection response*

In long-term selection, the response curve is expected to be exponential according to the theory of selection limits (Robertson, 1960; James, 1962, 1965). The observed response patterns generally conformed to this expectation in early stages of selection, except perhaps in CCa. Thereafter, however, individual lines responded in diverse patterns, which deviated from the expected curve in showing (1) irregular, unpredictable responses typically with periods of acceleration and quiescence (except in Ua), (2) linear responses at later stages of selection (Ua and CCb), and (3) abrupt attainment of plateaux (Ua, Ub and CRa).

The use of single-pair matings in G 68–76 seems to have been partly responsible for the abrupt levelling of response in Ua and Ub, as this might temporarily have reduced natural selection opposing artificial selection. The sudden plateau in CRa was perhaps due to selection for a lethal which had brought about the preceding rapid response as previously suggested for a similar pattern (Clayton & Robertson, 1957).

The steady and almost linear response observed in Ua and CCb in the second half of the selection experiment might be partly due to scale effect. But this pattern remained much the same even when the response was plotted against the cumulative selection differential to remove the scale effect. Although the persistent response would be most desirable in practice, it is very difficult to explain without further experimental evidence.

Accelerated responses have not been uncommon in many long-term selection experiments, particularly for various bristle number characters of *Drosophila* (for a review, see Jones *et al.* 1968). The present experiment conclusively shows that this kind of irregular response is more a rule than an exception, although the accelerated responses were individually rather unique and unpredictable. Also, most of the accelerated responses were accompanied by abrupt increase but no subsequent decrease in standard deviation; the distribution of bristle numbers tended to change a lot subsequently to the accelerated response. These observations together suggest that some major genetic factors were involved, which could not be brought to fixation by selection. The next paper (Yoo, 1980*a*) will in fact show that lethals having apparently large effects on bristle number had an important effect on this pattern of response.

(iii) *Characteristics of the lines at or near the selection limit*

Of the six replicate lines, three responded very little to selection in the last 10 or more generations. Had the selection been continued further, however, more renewed responses could have been obtained in these lines, as transitory quiescences lasting several generations had been observed earlier, for example G 44–53 in Ub. Although this possibility makes it difficult to judge whether selection limits were reached or being approached even after more than 85 generations of selection, the general characteristics of the lines observed at termination of selection were unlikely to change much under continued selection.

All the lines with the exception of Ua had become very unstable by the time selection was finally relaxed, in the sense that mean bristle number was fluctuating widely from generation to generation, reflecting the high phenotypic variability, and that the loss of genetic gain upon relaxed selection was rapid in the first few generations. In the extreme case of CRb, the loss after 7 generations amounted to more than 40% of total genetic gain. In addition, the distribution of bristle numbers was clearly bimodal (Ub, CRa and CCa) or skewed to the left (CRb and CCb). These characteristics are all consistent with the fact that lethals with large effects on bristle number kept segregating under selection as shown in the next paper (Yoo, 1980*a*).

(iv) *Variation among replicate lines*

The variation among replicates of total response is almost entirely dependent on the mean gene frequency over replicates at the limit, which in theory is a function of initial gene frequency and gene effect for a given selection regime (Robertson, 1960, 1970; Latter, 1969). Hence, it has been interpreted as indicating certain genetic properties of the base population and of observed selection responses (Jones *et al.* 1968; Comstock, 1973; Falconer, 1973; Enfield, 1977).

The variance of total response was about 27 σ^2_A of the base population, much larger than most genetic models might account for, and this was likely to be increased further with continued selection. Even on the logarithmic scale, the variance was still considerably higher than expected from genetic drift alone. The replicate variation was revealed not only in total response, but in the individuality of response patterns, variation of the sex-dimorphism ratio and different effects of sc^+ on abdominal bristle number (Yoo, 1974*b*). Also, the lethals and visible mutants affecting bristle number were largely non-allelic among the replicate lines (Yoo, 1980*a*).

The diversity of replicate variation, all concerned with one character, suggests that abdominal bristle number possibly is influenced by a large number of genes, but a smaller subset of these genes, substantially different among the lines, was responsible for selection response in any particular line. The frequency of some high bristle number genes in the base population might have been less than intermediate, perhaps even rare, as with genes at intermediate to high frequencies, the replicate variation of response would have been smaller than expected from genetic

drift alone (Kojima, 1961). This interpretation is consistent with the postulation of genes initially at low frequencies as a possible source of genetic variability remaining after many generations of relaxed selection (Yoo, 1980*b*). A similar suggestion was made on different grounds in a selection experiment with essentially the same base population (Jones *et al.* 1968).

Jones *et al.* (1968) observed that replicate variation tended to decrease as the number of parents selected was increased from 10 to 40 pairs. It was therefore expected that with a larger population size, replicate lines would be more alike in long-term response and selection limit. In fact, however, the variability of long-term response appeared to be no less in the present experiment than in other replicated selection experiments of similar nature with smaller population sizes (Clayton & Robertson, 1957; Sheldon, 1963; Jones *et al.* 1968).

In conclusion, the selection response continued for at least 75 generations, showing diverse, unpredictable patterns typically with one or more accelerated responses in later generations. The total response was great (more than 3 times the base population mean), but unlikely to exceed $N_e \Delta G_1$ at the limit. Variation among replicates was very large and at termination of selection, most of the lines appeared to be segregating for non-fixable genes with large effects on bristle number.

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