

Selection for a threshold character in *Drosophila*

II. HOMEOSTATIC BEHAVIOUR ON RELAXATION OF SELECTION

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1. INTRODUCTION

In the first paper of this series (Latter, 1964) it was suggested that scutellar bristle number in *Drosophila* may be an extremely useful model character for experiments in quantitative genetics. The response to artificial selection in the Canberra population was shown to be continuous over the period of generations required to increase mean bristle number in females from four to six, and both the realized heritability and phenotypic variance measured on the underlying scale remained unchanged throughout this initial response phase.

An analysis of the phenotypic variance on the underlying scale showed that scutellar bristle number is similar in some respects to the two characters most frequently used in selection experiments with *Drosophila*, viz. abdominal and sternopleural hair number. The realized heritability of total bristle score on the underlying scale is 0.33 ± 0.01 in the Canberra population, and the character is influenced only slightly by environmental variation under standard conditions. The major source of non-genetic variance was shown to be 'developmental error'.

Quite apart from the ease with which the trait may be scored, scutellar bristle number has the additional advantage for experimental purposes of showing pronounced genetic homeostatic behaviour on relaxation of artificial selection (Latter, 1963). Its use in selection studies therefore focuses attention on the possible effects of loci on the overall reproductive fitness of the organism, in addition to their direct effects on the selection criterion itself. In the present communication it is proposed to describe (i) the pattern of response in lines derived from the Canberra population by artificial selection for increased scutellar bristle number; (ii) the homeostatic behaviour of the lines on relaxation of artificial selection; and (iii) correlated changes in competitive ability, reproductive capacity, and rate of development in the selected populations.

2. CHANGES IN MEAN ON THE PROBIT SCALE

The regimes of selection involved in the three lines Sc 1, Sc 2 and Sc 3 have previously been described (Latter, 1964). In Sc 1 and Sc 3 the offspring of selected parents were raised in single-bottle cultures each generation, the harmonic mean number of parents approximating 20 pairs over the first 10-generation period.

Artificial selection was thereafter discontinued in Sc 1, and its competitive ability relative to that of a contemporary control population was studied in some detail. In Sc 3 selection was continued for a further 37 generations with a mean of 26 pairs of parents per generation. Selection line Sc 2, on the other hand, involved 50 single-pair matings of selected females with randomly chosen males each generation, each full-sib group being raised in a single vial. After 20 generations of this regime the line was maintained in single-bottle cultures for a further 30 generations of artificial selection, with an average of 27 pairs of parents per generation.

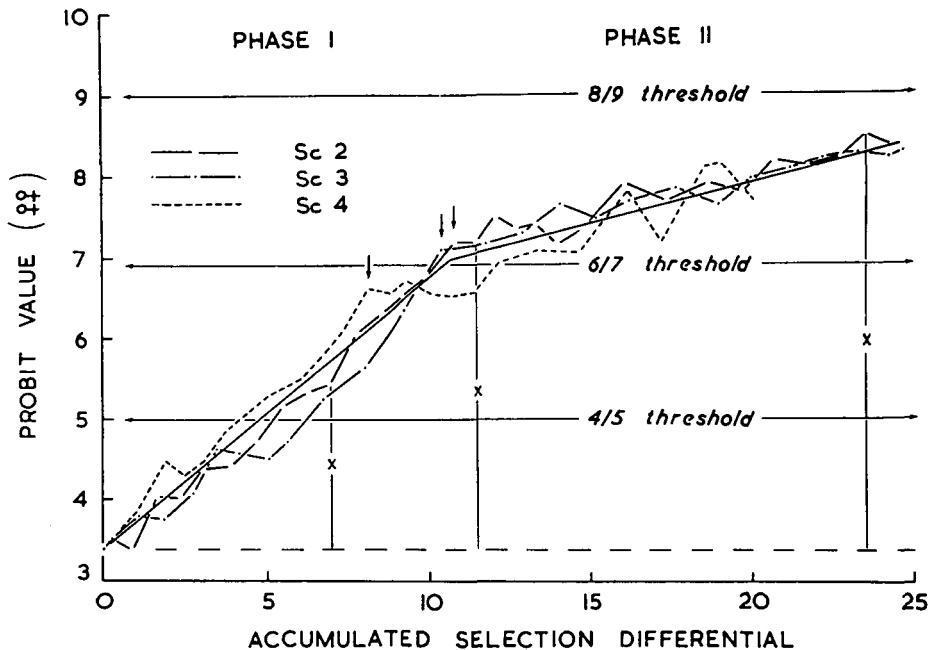


Fig. 1. The pattern of response to selection for bristle number measured on the underlying probit scale. The arrows indicate the point at which phase II was considered to have begun in each selection line. Crosses indicate the means of backcrosses to the base population.

A fourth selection line was extracted from the Canberra base population 90 generations after its introduction into the laboratory (Sc 4). The regime of selection was similar to that practised in Sc 1 and Sc 3, offspring again being raised in single-bottle cultures each generation. Over a 23-generation period of selection the number of parents per generation averaged 25 pairs.

The response to selection in females of lines Sc 2, Sc 3 and Sc 4, extending over a period of generations corresponding to an accumulated selection differential ($\Sigma \bar{i}_u$) of 25 units, is shown in Fig. 1. The means of the populations are plotted on the probit scale according to the following convention. As in Fig. 1 of Latter (1964), a population with females having a mean bristle number in the range 4–6 has been plotted relative to the position of the 4/5 threshold, which corresponds to a probit value of 5.0. The total probit distance spanned by the 5- and 6-bristle classes is

1.9 units in populations recently derived from the base population by selection (Latter, 1964), and a population with a mean bristle number in the range 6–8 has been plotted relative to the location of the 6/7 threshold (6.9 units). The 8/9 threshold is also indicated in Fig. 1, the probit distances spanned by the 7- and 8-bristle classes having been estimated from generations 10–20 of Sc 2, where approximately 500 female offspring were scored each generation. The distances are 0.90 ± 0.03 and 1.22 ± 0.06 probits for the 7- and 8-bristle classes respectively.

The most striking feature of the response curves in Fig. 1 is the clear evidence of two distinct phases of response in each of the three lines, the zone of transition from one phase to the next approximating to the position of the 6/7 threshold on the underlying scale. The realized heritability in the direction of selection averaged 0.34 ± 0.01 through phase I, and 0.10 ± 0.01 in phase II, there being no evidence of non-linearity in either phase. There can be little doubt of the repeatability of the phenomenon, in spite of the significant heterogeneity of the estimates within each of the two response phases (Table 1).

Table 1. *Realized heritability (h^2) in phases I and II of the response to selection*

Line	Phase I		Phase II	
	$\Sigma \bar{v}_u$	h^2	$\Sigma \bar{v}_u$	h^2
Sc 2	0.0–10.8	0.35 ± 0.01	10.8–24.3	0.09 ± 0.01
Sc 3	0.0–10.4	0.30 ± 0.03	10.4–24.6	0.09 ± 0.01
Sc 4	0.0– 8.1	0.37 ± 0.02	8.1–20.0	0.13 ± 0.02
Means	0.0– 9.8	0.34 ± 0.01	9.8–23.0	0.10 ± 0.01

Also depicted in Fig. 1 are the means of backcrosses of line Sc 2 to the base population after 10, 16 and 29 generations of selection. In each case the mean of the hybrid population is close to the arithmetic mean of the corresponding parental values, so that the probit scale may be taken to be satisfactory throughout the entire range of values under consideration. In populations with mean probit values in the range 5.5–8.0, total bristle score is essentially normally distributed with phenotypic standard deviation equal to unity (Table 2). Within this range the bristle number and probit scales are therefore virtually identical apart from the change in origin of one-half a unit.

Table 2. *The regression of the standard deviation of total bristle number on the value of $\Sigma \bar{v}_u$, for populations with mean probit values in the range 5.5–8.0*

Line	Regression coefficient	Mean phenotypic standard deviation (σ)
Sc 2	-0.005 ± 0.005	1.03 ± 0.02
Sc 3	0.000 ± 0.007	1.00 ± 0.03
Sc 4	-0.006 ± 0.004	0.95 ± 0.02
Means	-0.004 ± 0.003	0.99 ± 0.02

If the regime of artificial selection is discontinued, and the population maintained by random mating under crowded conditions with more than 100 pairs of parents in a single culture each generation, an appreciable proportion of the gain made under selection is rapidly lost. Fig. 2 shows the regression of the mean in line Sc 2 on relaxation of selection at generations 16, 23 and 33. The curve for Sc 2/16/R is the average of two independent replicate populations which behaved almost identically. It can be seen from Table 3, however, that the rate of change in the mean is not the same for all of the four selection lines when relaxed at the same level, the phenomenon being most marked in Sc 1 and Sc 2 when artificial selection was discontinued at the beginning of phase II. Note that the mean probit values given in Fig. 2 and Table 3 are based on the bristle scores of samples of individuals raised under optimal conditions, so that the effect of crowding on the expression of the character is not involved.

Table 3. *Changes in mean probit value on relaxation of artificial selection. The base population mean on the probit scale is 3.4 units*

Mean probit value	Population	Mean after relaxation for		Proportionate return to base level (%)
		10 gens.	25 gens.	
5.5	Sc 4/7*	5.0	4.8	30
6.7	Sc 4/12	6.0	5.6	32
7.1	Sc 4/17	6.6	6.4	18
7.2	Sc 2/16	5.8	5.6	43
7.3	Sc 1/10	6.1	5.8	39
7.3	Sc 3/13	6.4	6.4	24
7.7	Sc 2/23	7.0	6.6	25
8.2	Sc 3/21	7.2	7.2	21
8.5	Sc 2/33	7.8	7.7	13

* Denotes the population resulting from 7 generations of selection in line Sc 4.

In view of this pronounced homeostatic behaviour of the mean of selected populations on relaxation of selection, one must consider two possible explanations of the change in realized heritability at the end of phase I. There may be (i) a change in the magnitude of the additive genetic variance in the population on reaching the 6/7 threshold, and/or (ii) an intensification of forces tending to reduce the *realized* advance under selection. Direct measurements of the potential response to selection at various stages in selection line Sc 2 suggest that both phenomena are of importance.

Throughout the period of generations from Sc 2/9–14, i.e. the latter half of phase I in this line, approximately 50 pair-matings of randomly chosen individuals were set up each generation, and the female offspring scored for bristle number. The regression of offspring mean on female parent, based on the untransformed bristle counts, was 0.21 ± 0.02 averaged over the 6-generation period, and the corresponding mean full-sib correlation coefficient was 0.22 ± 0.02 . The two estimates are in close agreement (though they are not statistically independent),

suggesting that the genetic variance in bristle count is almost entirely additive. The predicted heritability in phase I is therefore 0.42 ± 0.04 .

Estimates of the additive genetic variance present in Sc 2 during phase II have been derived from the results of two-way selection commenced in generations Sc 2/18 and 27, extending over periods of 3 and 5 generations respectively. The pooled estimate of heritability from these two experiments, as judged from the divergence between the high and low selection lines is 0.23 ± 0.03 . Comparison with the estimate for phase I (0.42 ± 0.04) indicates an average reduction in the

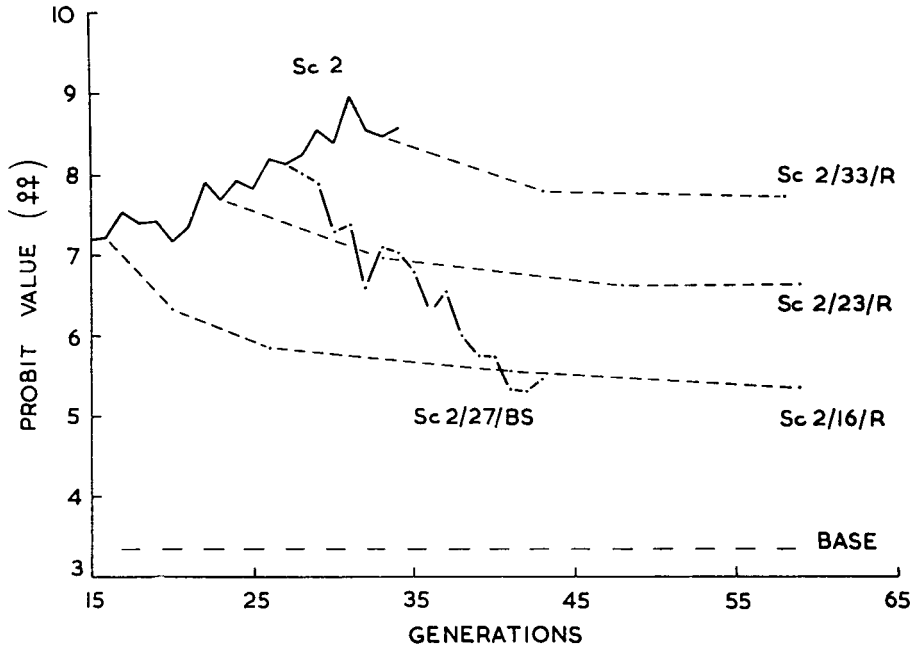


Fig. 2. The behaviour of selection line Sc 2 on relaxation of selection (R) and under back selection (BS) in phase II.

additive genetic standard deviation of approximately 25%. However, the comparisons set out in Table 4 show that whereas the *realized* response to selection in phase I is roughly 80% of that predicted as a function of the additive genetic variance, the realized response in the positive direction in phase II represents only 43% of the potential response. The part played by natural selection during these two phases is to be considered in some detail in the next section.

Table 4. *Comparison of potential and realized response to selection for increased scutellar bristle number*

Phase of response	Heritability	
	Potential	Realized
I	0.42 ± 0.04	0.34 ± 0.01
II	0.23 ± 0.03	0.10 ± 0.01

3. CORRELATED CHANGES IN REPRODUCTIVE FITNESS

A detailed examination of the competitive ability of individuals is selection line Sc 1 was made after 10 generations of artificial selection, using a technique based on that proposed by Knight & Robertson (1957). The test involves competition between a group of 25 virgin individuals of each sex from the wild-type population (+/+) and the same number from a mutant tester stock (Cy/Pm), chosen so that the progeny of cross-matings between the stocks can be identified. The wild-type and mutant genotypes are raised for the purpose in a common culture, care being taken that the two sets of competing adults are matched with respect to age.

The progeny emerging from the competition culture are of four types, viz. +/+ , Cy/+ , +/Pm, Cy/Pm. The ratio of +/+ to Cy/Pm has been termed by Knight and Robertson the *competitive index* relative to the tester stock, being a measure of the product MFS, where M denotes the relative mating ability of +/+ males, F the relative fecundity of +/+ females, and S the relative probability of survival to breeding age. The ratio of half the number of 'crossbred' progeny (i.e. Cy/+ and +/Pm) to the number of Cy/Pm offspring similarly measures $\frac{1}{2}S^*(M+F)$, where S* denotes the mean probability of survival of the hybrid genotypes expressed in relative terms.

In the present study, a supplementary test has been used to measure the ratio of S to S*, under comparable conditions to those prevailing in the previous test. A combined measure of the *relative fitness* of the wild-type population can then be derived, i.e. $\frac{1}{2}S(M+F)$. A set of 25 +/+ females, previously mated to +/+ males, was placed in competition with a matched set of +/+ females previously mated to Cy/Pm males. The ratio of +/+ to crossbred progeny emerging from the culture has been taken as a measure of S/S*. It should be stressed, however, that this modification of the test devised by Knight and Robertson is strictly applicable only if (i) the sex chromosome has a small effect on the survival of crossbred males, and (ii) there is a negligible frequency of active, sterile males in the wild-type stock under test.

Table 5. *Competitive indices and measures of fitness relative to a Cy/Pm tester stock, for selection line Sc 1 after 10 generations of artificial selection*

Population	MFS†	$\frac{1}{2}S^*(M+F)$	S/S*	$\frac{1}{2}S(M+F)$
Canberra	2.93 ± 0.20 (100)	2.19 ± 0.11 (100)	1.00 ± 0.04 (100)	2.19 ± 0.14 (100)
Control	2.02 ± 0.27 (69)	1.79 ± 0.16 (82)	0.99 ± 0.06 (99)	1.77 ± 0.19 (81)
Sc 1/10	0.80 ± 0.09 (27)	0.88 ± 0.08 (40)	1.07 ± 0.07 (107)	0.95 ± 0.10 (43)

† Symbols M, F, S and S* refer to male mating ability, fecundity in the female, and survival of purebred and crossbred progeny respectively. The figures in brackets express all results in terms of the Canberra population as 100.

In Table 5 are presented the measures of competitive ability which were obtained in the study of Sc 1, together with their standard errors calculated from the observed variance among replicate tests. The populations concerned are the Canberra base

population, selection line Sc 1/10, and a contemporary control population maintained with the same number of breeding individuals randomly chosen each generation. The reduction in reproductive fitness in the selection line is quite appreciable when one considers that only 10 generations of artificial selection had been practised, bringing the mean on the probit scale from 3.4 up to 7.3 in females, i.e. to the beginning of phase II of the response curve (Fig. 1). The fitness of the selected population relative to the control can be estimated to have been 0.54 ± 0.08 .

In the light of these observations, selection line Sc 2 was designed (i) to provide a measure each generation of the reproductive capacity of a random sample of individuals from the selection line, so that the pattern of the correlated response

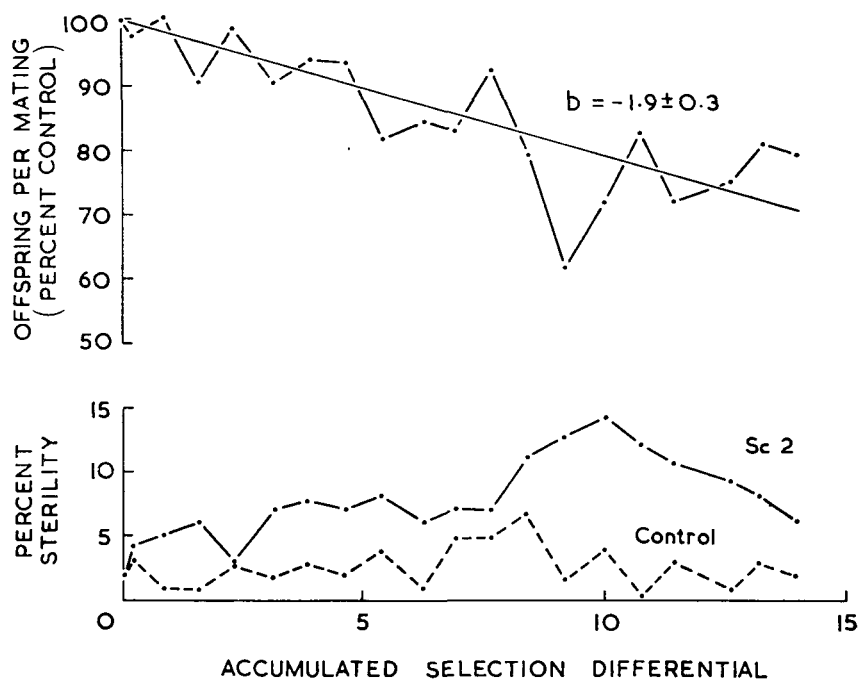


Fig. 3. The decline in mean number of offspring per pair mating in selection line Sc 2, expressed as a percentage of the control population. The incidence of sterile cultures is also plotted, a sterile culture having been defined as one producing fewer than 20 offspring.

in fitness could be ascertained, and (ii) to reduce the degree of inbreeding in the selected population to as low a level as possible. Robertson (1961) has shown that the rate of inbreeding under artificial selection is expected to be greater than that in a random-bred control, due to the fact that breeding individuals tend to be drawn predominantly from progeny groups with high mean performance, particularly when the heritability of the character is high. Fifty pairs of parents were involved in Sc 2 each generation, one male being randomly chosen from each of the 50 full-sib groups, while a selection intensity of 50/500 was applied to females initially drawn in equal numbers from the 50 families.

In addition, a random sample of 100 individuals of each sex was taken from the selection line each generation to provide a measure of average *reproductive capacity* under optimal conditions, i.e. total number of offspring per pair mating in a single 4 in. \times 1 in. vial. The random and selected sets invariably had some full-sib family groups in common. For comparison, a set of 100 pair matings of individuals representative of the Canberra population was scored for offspring number each generation, all parental individuals having been raised under optimal conditions in vials.

The observed reduction in reproductive capacity in Sc 2 is shown in Fig. 3. In each generation the counts have been expressed as a percentage of the corresponding mean observed for the Canberra population, which varied over the period from 133–226 with a mean of 176 offspring per pair. The graph supports the view that the reduction in fitness begins with the first few generations of artificial selection for increased bristle number, and is almost constant throughout phase I. The rate of decline in reproductive capacity under optimal conditions is of the order of 2% per unit increase in the accumulated selection differential (Fig. 3). The available evidence suggests that this rate of decline is maintained through to the end of phase II, generation Sc 2/33 having been observed to produce 53% as many offspring as the base population under these same test conditions (Table 8). The value of $\Sigma \bar{v}_u$ for Sc 2/33 is 27.2, i.e. a little beyond the range of Fig. 1.

Female sterility, fecundity and generation interval

In the study of homeostatic behaviour in Sc 2/16/R (Fig. 2), a separate population was maintained with 50 pairs of parents randomly mated in vials each generation, one male and one female being taken whenever possible from each of the full-sib groups. Over a period of 6 generations, the mean of this population regressed by 0.8 probits compared with a mean change of 1.1 probits in the two lines maintained by mass-mating. Approximately 70% of the loss in response in the mass-mated populations can therefore be attributed to a combination of the following factors: (a) linkage disequilibrium in the selected population (Latter, 1963); (b) natural selection among families due to sterility; and/or (c) natural selection operating on the genetic variability in fitness *within* full-sib family groups.

There is no information on the possible importance of the first of these effects. A detailed study of selection line Sc 2 has shown, however, that sterility is a major factor in the loss of reproductive capacity under continued artificial selection (Fig. 3). The level of sterility in pair matings rose to 14% in Sc 2 at the zone of transition from phase I to phase II, compared with a mean incidence of 3% in the control population. By generation Sc 2/33, corresponding to the end of phase II, the mean incidence of sterility had risen to $20 \pm 4\%$. A study of outcrosses using males from the base population has indicated that it is the female parent which is showing the high degree of sterility (Table 6). The reduction in number of offspring per *fertile* culture can also be seen to be due in part to components other than female fecundity, i.e. to reduced male fertility or to an increase in mortality.

Twenty-six per cent of the loss in reproductive capacity is recovered on outcrossing females of Sc 2.

Table 6. *Measures of reproductive capacity in outcrosses of Sc 2 females to males of the Canberra base population*

Type of mating	Sterile cultures (%)*	Mean number of offspring per fertile culture
Sc 2/10 × Sc 2/10	7.0 ± 2.6	153 ± 4
Sc 2/10 × Base	12.0 ± 4.6	171 ± 7
Base × Base	2.9 ± 0.3	186 ± 3
Sc 2/16 × Sc 2/16	10.4 ± 2.6	141 ± 5
Sc 2/16 × Base	12.0 ± 4.6	164 ± 7
Base × Base	2.9 ± 0.3	200 ± 3

* A culture derived from the mating of a single pair has been classed as sterile if fewer than 20 offspring were produced.

Selection in favour of early-emerging individuals has also been identified as an important factor in the homeostatic behaviour of populations on relaxation of artificial selection. Commencing with Sc 2/27, two populations were maintained by continued breeding from 25 pairs of the earliest (E) or of the latest (L) emerging individuals from a single bottle culture each generation. No selection for scutellar bristle number was practised in either of the populations. The E line showed a rapid fall in mean probit value over the first 10 generations of the regime, whereas the mean of the L line was almost unchanged at the end of this period. Thereafter the mean of both lines declined at approximately the same rate (Table 7).

Table 7. *The correlated response in mean probit value for scutellar bristles, in populations derived from Sc 2/27 by continued selective breeding from early (E) and late (L) emerging individuals*

'Early' selection		'Late' selection		Correlated response
Generation	Probit value	Generation	Probit value	
E 0	8.1	L 0	8.1	0.0
E 4	7.3	L 4	8.1	0.8
E 11	6.7	L 10	7.9	1.2
E 18	6.2	L 15	7.2	1.0
E 27	6.4	L 22	7.4	1.0

In all the selection lines and mass-mated populations involved in this study, the standard routine has been to take the required number of individuals for scoring, or for breeding, from among the first to emerge from the parental cultures. Natural selection for a reduced generation interval will therefore operate to retard progress in lines under artificial selection, and will contribute towards a regression of the mean on relaxation of selection. However in the pedigreed population maintained from Sc 2/16 by pair matings each generation, natural selection for rate of development

would be restricted to the available *within-family* variability, and would therefore be reduced in effect by a factor of one-half (Gowe *et al.*, 1959). In the same way the scope for natural selection for rate of development in Sc 2 would have been somewhat reduced over the period Sc 2/1-20, since males for breeding were taken equally from each full-sib family throughout this period.

Further information on this component of fitness is presented in Table 8, together with measures of sterility, fecundity, and competitive ability in a number of populations tested in a single comparative experiment. The competitive indices in this table were obtained from tests involving inseminated females of the wild-type stock and a white-eyed tester stock, and do not therefore take male mating ability into account (Latter & Robertson, 1962). The following populations were studied: (1) the Canberra base population with a mean probit value in females of 3.4; (2) selection line Sc 4 after 6 generations of selection, the mean probit value then being 5.3; (3) Sc 2/16 after relaxation of artificial selection for a period of 18 generations, during which the mean probit value had dropped from 7.2 to 5.7; (4) Sc 1/10 following 80 generations of relaxation, the population being stable at this stage with a mean of 5.3 on the probit scale, whereas the level prior to relaxation had been 7.3 probits (Table 3); (5) selection line Sc 2 after 33 generations of continuous artificial selection, the mean probit value being 8.5; and (6) a line in which selection for increased bristle number had been practised for 31 generations, the initial population being Sc 1/10/R48. A detailed account of the selection response in this last line is beyond the scope of the present paper: it is sufficient for our purpose to note that the mean *bristle number* in females of the line had been increased to more than 10, compared with a mean in Sc 2/33 of almost exactly 8 bristles.

Table 8. *Components of reproductive ability in contemporary populations. The history of each population is summarized in the text*

Population	Sterile cultures (%)	Offspring per fertile pair	Rate of development*	Competitive index (♀)†
(1) Canberra base	2.9 ± 0.3	164 ± 4	31.5 ± 0.9	1.00
(2) Sc 4/6	3.0 ± 1.7	175 ± 4	22.2 ± 0.8	0.68 ± 0.13
(3) Sc 2/16/R18	4.1 ± 2.0	171 ± 4	21.8 ± 0.9	0.53 ± 0.10
(4) Sc 1/10/R80	3.0 ± 1.7	154 ± 4	17.4 ± 1.0	0.38 ± 0.07
(5) Sc 2/33	19.8 ± 3.9	107 ± 4	18.3 ± 1.6	0.17 ± 0.03
(6) Sc 1/10/R48/S31	3.1 ± 1.7	127 ± 4	15.4 ± 1.2	0.22 ± 0.04

* Measured as the mean number of offspring per fertile pair emerging within ten days of initiation of the cultures, expressed as a percentage of the total emergence.

† Expressed relative to that of the Canberra base population.

Perhaps the most surprising feature of Table 8 is the clear-cut demonstration of a reduction in 'rate of development' after only 6 generations of artificial selection for bristle number in Sc 4. There was no detectable increase in the frequency of sterile cultures at this stage, nor was there a significant reduction in the reproductive

capacity of fertile individuals under optimal conditions. The competitive index showed a reduction which was on the borderline of statistical significance.

It is also instructive to compare the fitness components of populations (3) and (4) in Table 8 with those of Sc 4/6, bearing in mind that these three populations were at almost precisely the same mean probit value at the time of testing. From Fig. 3 it can be seen that the level of sterility in Sc 2/16 had risen to roughly 10% under artificial selection, and the mean number of offspring per *fertile* pair was approximately 85% that of the control population. Relaxation for 18 generations resulted in a population comparable in most respects with Sc 4/6. However, Sc 1/10/R80 made only a partial recovery despite the fact that its history is similar to that of Sc 2/16/R18, i.e. artificial selection up to a probit value of 7.3 followed by an extended period of relaxation. The level of sterility in Sc 1/10/R80 was comparable to that of Sc 4/6, but 'rate of development' and the mean productivity of fertile pairs were both significantly lower, as was the competitive index.

There is therefore clear evidence of the *fixation* of deleterious genes in selection line Sc 1 during a period of only 10 generations of selection for bristle number. Random fixation of genes due to restricted population size alone may have played a part in this process, but it is more likely that directed changes due to artificial selection have been responsible. The behaviour of selection line Sc 2 on relaxation of selection in phase II lends support to the latter view. Though the rate of response in mean probit value is approximately linear in this phase, it is nevertheless clear from Fig. 2 that fixation of deleterious alleles is being effected by artificial selection in Sc 2 throughout phase II, the total regression of the mean on relaxation of selection being considerably less at the end of the period than at the beginning (Table 3).

Continuous selection in Sc 2 can be seen from Table 8 to lead to an extremely high incidence of sterility, and to pronounced changes in fecundity and rate of development, despite the large effective breeding size of the population throughout. Comparison with population (6), which has a much higher mean bristle score than Sc 2/33, demonstrates the possibility of producing individuals of high mean performance for bristle number, with conspicuously improved reproductive capacity compared with those resulting from continuous selection. Some of the difficulties involved in realizing this objective are to be discussed in the next paper of this series.

4. DISCUSSION

One of the features of the results presented in this paper is the regularity of the pattern of response to selection, and the repeatability of associated changes in components of reproductive fitness. The study has been designed to minimize the effects of genetic sampling from generation to generation, and also to limit as far as possible the part played by linkage in correlated responses to artificial selection. The foundation population was based on more than 100 pairs of individuals derived from a single extensive collection made in the wild, and has been maintained under

competitive conditions in the laboratory with roughly 500 pairs of parents per generation.

Selection line Sc 1 was extracted from this population after only 7 generations, but a period of 60 generations elapsed before the initiation of lines Sc 2, 3 and 4. During this period linkage equilibrium should have been established for all but the most tightly linked genes. Correlated changes in fitness under selection for bristle number may therefore be considered to be due to pleiotropy of the units of segregation in the base population, though we must always allow for the possibility that a rare recombinational event may lead to occurrences which appear to be unique.

Under artificial selection for increased scutellar bristle number, progress from the base mean of 4.05 bristles in females to one approaching 8 bristles has been shown to involve two distinct phases (Fig. 1). During phase I the response on the underlying probit scale is effectively linear, the mean increasing to a level which corresponds closely to the position of the 6/7 threshold. The realized response during this phase is 0.34 ± 0.01 probits per unit increase in the accumulated selection differential, whereas the corresponding estimate of 'potential' response, based on parent-offspring and full-sib correlations, is 0.42 ± 0.04 probits.

During phase I there is a progressive reduction in the reproductive capacity of randomly chosen individuals as selection proceeds (Fig. 3), one of the important factors being an increase in the incidence of sterility among females. A significant increase in generation interval can also be detected after only 6 generations of artificial selection (Table 8), and a considerable proportion of the gain in bristle number is lost on relaxation of selection during this phase (Table 3). Natural selection is then presumably opposing artificial selection even in this initial response phase, and we can roughly estimate the loss in response to be of the order of 20% (Table 4). The analysis of variation in scutellar bristle number presented in the first paper of this series, being based on estimates of the realized heritability, has therefore probably underestimated the magnitude of the additive genetic variance present in the base population.

The rate of response to selection for increased bristle number in phase II is also approximately linear, the realized heritability being 0.10 ± 0.01 , i.e. roughly 30% of that observed during the first phase (Fig. 1). Two-way selection experiments in phase II have suggested that the 'potential' response during this phase corresponds to a heritability of 23%, the realized heritabilities in the plus and minus directions being 10 and 36% respectively. Estimates of additive genetic variance in populations subject to the influence of natural selection must of course be treated with some caution, particularly if genes of large effect are involved. It nevertheless appears likely that the reduced rate of response in phase II, by comparison with that observed in phase I, is due partly to an average reduction of something like 25% in the additive genetic standard deviation in populations whose mean has been pushed beyond the 6/7 threshold. Note, however, that there was no detectable change in the phenotypic variance observed for total bristle number (Table 2).

The loss in response due to the opposition of natural selection (as judged from the behaviour of populations on relaxation of artificial selection), also reaches a

maximum near the zone of transition from phase I to phase II (Table 3). Thereafter, the progressive fixation of deleterious alleles throughout phase II leads to a lessening of homeostatic behaviour on relaxation of artificial selection (Fig. 2), and to marked changes in mean number of offspring per fertile pair, rate of development, and competitive ability. The incidence of female sterility in Sc 2 has also been observed to rise to a level of 20% during this phase (Table 8).

The evidence of fixation of 'plus' alleles after only 15–35 generations of moderately intense selection suggests that a small number of loci of large effect on both bristle score and reproductive fitness are involved, making their maximum contribution to the additive genetic variance in fitness at an accumulated selection differential of roughly 10 units. A quantitative assessment of the probable magnitude of effect of these loci is to be published elsewhere (Latter, 1967), but genes of effect roughly equal to the phenotypic standard deviation seem likely to be involved. The response to back selection from phase II populations (for example Sc 2/27/BS in Fig. 2) suggests that in addition to these major loci, a number of minor loci are contributing to the genetic variance present in phases I and II, and that these loci of small effect are nearly neutral as far as reproductive fitness is concerned. The results of back selection in populations which have stabilized under natural selection (for example Sc 1/10/R48) point to the same conclusion, as will be discussed in the next paper of this series.

If we are correct in inferring the existence of a number of loci of large effect in addition to the usual background of minor genes, it should be possible to identify some of these by means of techniques similar to that suggested by Thoday (1961), and to characterize the effects of the genes individually and in combination. Experiments along these lines are currently in progress.

SUMMARY

This paper is concerned with three related aspects of the behaviour of populations under artificial selection for increased scutellar bristle number: (i) the pattern of response on the probit scale; (ii) the homeostatic behaviour of the selection lines on relaxation of artificial selection; and (iii) correlated responses in generation interval, reproductive capacity and competitive ability. The study was designed so that linkage would be a comparatively unimportant factor in promoting correlated responses to selection, and the effects of genetic sampling from generation to generation were also reduced to a low level.

Progress from the base mean of 4.05 bristles in females to a level of almost 8 bristles has been shown to involve two distinct phases with realized heritabilities of 0.34 and 0.10 respectively, the zone of transition corresponding closely to the position of the 6/7 threshold on the underlying scale. In addition to an apparent average reduction of about 25% in the additive genetic standard deviation in phase II by comparison with phase I, the loss in response due to the opposition of natural selection has been shown to reach a maximum near the zone of separation of the two phases.

The pattern of behaviour of the populations under artificial and natural selection has suggested the presence in the base population of genes of large effect on both bristle number and reproductive fitness. There is also evidence of additional genetic variation in bristle number which is effectively neutral with respect to fitness. Continued selection for increased scutellar bristle number in large populations has been shown to reduce mean competitive ability by more than 80%.

REFERENCES

- GOWE, R. S., ROBERTSON, A. & LATTER, B. D. H. (1959). Environment and poultry breeding problems. V. The design of poultry control strains. *Poult. Sci.* **38**, 462–471.
- KNIGHT, G. R. & ROBERTSON, A. (1957). Fitness as a measurable character in *Drosophila*. *Genetics*, **42**, 524–530.
- LATTER, B. D. H. (1963). Genetic homeostasis and the theory of canalization. In *Statistical Genetics and Plant Breeding* (W. D. Hanson & H. F. Robinson, eds.), pp. 455–467. National Academy of Sciences—National Research Council Pub. 982.
- LATTER, B. D. H. (1964). Selection for a threshold character in *Drosophila*. I. An analysis of the phenotypic variance on the underlying scale. *Genet. Res.* **5**, 198–210.
- LATTER, B. D. H. (1967). The response to artificial selection due to autosomal genes of large effect. IV. The increase in frequency of deleterious recessive genes in finite populations. *Aust. J. biol. Sci.* (in press).
- LATTER, B. D. H. & ROBERTSON, A. (1962). The effects of inbreeding and artificial selection on reproductive fitness. *Genet. Res.* **3**, 110–138.
- ROBERTSON, A. (1961). Inbreeding in artificial selection programmes. *Genet. Res.* **2**, 189–194.
- THODAY, J. M. (1961). Location of polygenes. *Nature, Lond.* **191**, 368–370.