The effect of different selection intensities on selection response in egg-laying of *Tribolium castaneum*

By R. G. RUANO, F. OROZCO AND C. LÓPEZ-FANJUL

Departamento de Genética, Instituto Nacional de Investigaciones Agrarias, Avda. Puerta de Hierro s/n, Madrid – 3, Spain

SUMMARY

An experiment was carried out to test the effect of varying selection intensity on the response to individual selection with a fixed number of individuals scored per generation. The selected trait was egg laying of virgin females of *Tribolium castaneum* scored from the 7th to the 11th day after adult emergence. Five different selected proportions of females were considered (5, 10, 20, 33 and 50 %) and each treatment was represented by two replicate lines. Control lines were maintained throughout the experiment. The lines selected at the lowest proportions (5 and 10 %) led to the largest initial gains, but the largest final gains were achieved by the lines where the proportions selected were 10 and 20 %, in agreement with theory. Lines where the proportion selected was 50 % gave the lowest rate of response over the period considered (32 generations). A good agreement was found between predicted and realized short-term responses to selection. Prediction at later stages of selection deteriorated in the most strongly selected lines mainly due to the levels of inbreeding attained.

1. INTRODUCTION

The influence of selection intensity on the rate of response is of importance in selection programmes. In a practical breeding programme neither short- nor long-term response can be considered as the only operative criterion. Smith (1969) and Robertson (1970) have shown theoretically that for a given constant number of individuals scored per generation, there is an optimum selection intensity which maximizes the selection gains achieved in a fixed number of generations. In agreement with theory, Jones, Frankham & Barker (1968) selecting *Drosophila* for high abdominal bristle number in lines with the same total number of individuals scored per generation, found that long-term response increased as a selection intensity decreased. Similar results have been reported by Hanrahan, Eisen & Legates (1973) selecting for high post-weaning weight in mice.

The present experiment studies the response achieved by five sets of lines of *Tribolium castaneum* selected under five different intensities but with the same total number of individuals scored per generation. Although the selected trait – egg laying – can only be scored on females, it can be shown that the predictions from Robertson's (1970) model are also valid in this particular case. It is hoped to present the theoretical analysis in a separate paper.

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2. MATERIAL AND METHODS

The Consejo population is a pool of several wild populations captured near Madrid and has been maintained in cages in this laboratory at 33° from 1964 (Orozco & Bell, 1974).

The trait selected was egg laying of virgin females scored from the 7th to the 11th day after adult emergence. All lines in this experiment were kept at 70 % relative humidity and 33 °C. At this temperature egg laying is maximized during the 4-day period considered (Fuentes & Orozco, 1970). The culture medium consisted of 95 % whole wheat flour and 5 % dried brewer's yeast. In these environmental conditions, the selected trait has been shown to be highly correlated with egg laying of inseminated females in the Consejo base population (Orozco and Tagarro, 1969).

Table 1. *Family structure of lines and selection procedure*

Line*	Number of families scored per generation	Number of females per family†	Selection intensity in females (%)	Selected/scored females
A	10	20	5	10/200
B	20	10	10	20/200
C	40	5	20	40/200
D	66	3	33	66/198
E	100	2	50	100/200
F	200	1	100	200/200

* Each line was replicated twice.
† Males and females equally represented in each family.

From a sample of 1500 pupae of each sex from the population cage, a random sample of 200 males and 200 females was taken and individually mated at random in vials. From each of these 200 females, six male and six female offspring were obtained to form generation 0. Individuals in generation 0 were divided into six groups of size 400 (A, B, C, D, E and F) each group consisting of one male and one female from each of those 200 families. Each of those six groups was scored and selected according to the procedures shown in Table 1. From each group two replicated lines (I and II) were obtained from two sets of offspring from the selected matings in generation 0.

Individual selection was practised in each line on females, with the same number of males and of females being taken at random from that same line. Individual matings were made at random except that full-sib matings were avoided. All sets of lines were contemporaries during the whole experiment.

3. RESULTS

(i) *The base population*

The parameters of the base population are shown in Table 2.

Heritabilities have been calculated by full-sister correlation and daughter-dam regression analyses, this latter giving a smaller but not significantly different esti-

mate. Twice the difference between these heritabilities estimates the relative importance of the dominance and maternal effects plus a fraction of the epistatic effects (Dickerson, 1959). In our case this difference is 0·06, with an approximate standard error of 0.13.

Table 2. *Parameters of the base population*

Mean	19·03
Standard deviation (based on 1500 females)	0·31
Phenotypic variance:	
Within-family	117·53
Between-family	20·90
Total (based on 200 full-sister families of size 6)	138·43
Coefficient of variation (%)	56
Heritability ± s.e.	
Full-sister correlation	0·30 ± 0·06
Daughter–dam regression	0·27 ± 0·02

(ii) *The selection results*

The average egg laying rate plotted against generation number is presented for the individual replicates in Figs. 1 and 2. A general picture of the selection results in all lines (replicates pooled) is shown in Fig. 3.

Two replicates of a control (lines F) were maintained throughout the whole experiment. As the performance of the control shows no time trends (Fig. 2F), all calculations have been performed on the uncorrected data.

The coefficients of variation and the within-family, between-family and total phenotypic variances of the selected lines are shown in Fig. 4 with averages taken over replicates.

There was a considerable response to selection in all lines. In general, there was excellent repeatability between selected replicates with the exception of the A lines. For the same number of individuals scored, higher intensities of selection led to faster initial responses. Lines A and B were best and performed very similarly from the start, followed by lines C and D which also showed a similar trend. Lines E responded slowly to selection but at a more regular rate than the other lines. Although by the end of the experiment (generations 29–32) there were no significant differences between the mean egg laying of lines A, B, C and D, their ranking order was $C > B > A > D$. The average of the A replicates did not rank first in spite of those lines being selected with the highest intensity. This was due to the cessation of the response in replicate A-II from generation 15 onwards.

Considering the experiment as a whole, total and within-family phenotypic variances increased to 4–6 times their original value in all lines. This increase in variance reached a maximum at around generation 10, when about 50 % of the total response had been achieved in all lines. Between-family variances also increased with selection although the changes per generation were of a more erratic nature
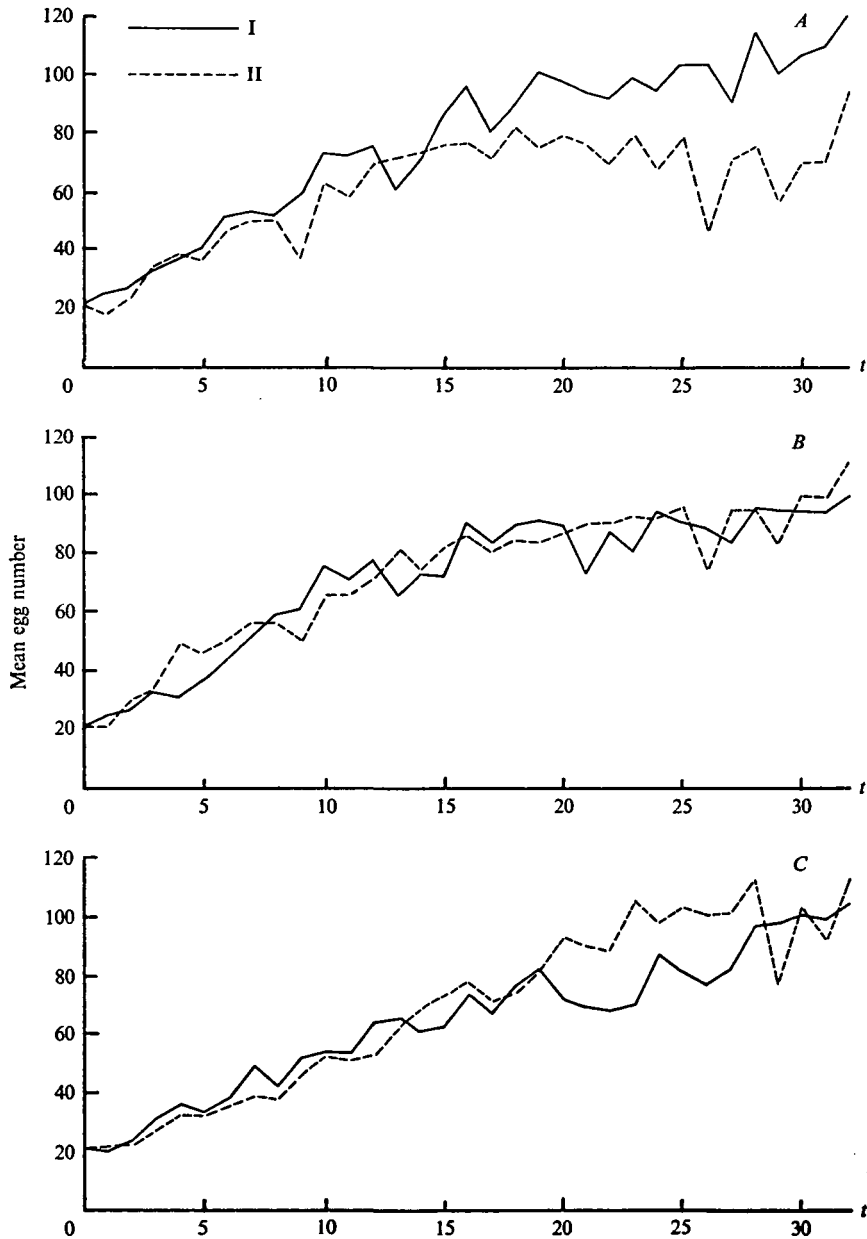
Fig. 1. Scores on *A*, *B* and *C* replicates.

than in the other variances estimated. These changes in the variances were less marked in line E. The coefficients of variation decreased to half their original values in all lines. Although the control means (F lines) did not present any directional trends throughout the experiment, both the total phenotypic variance and the coefficient of variation showed a small increase, unassociated with any known culture changes.
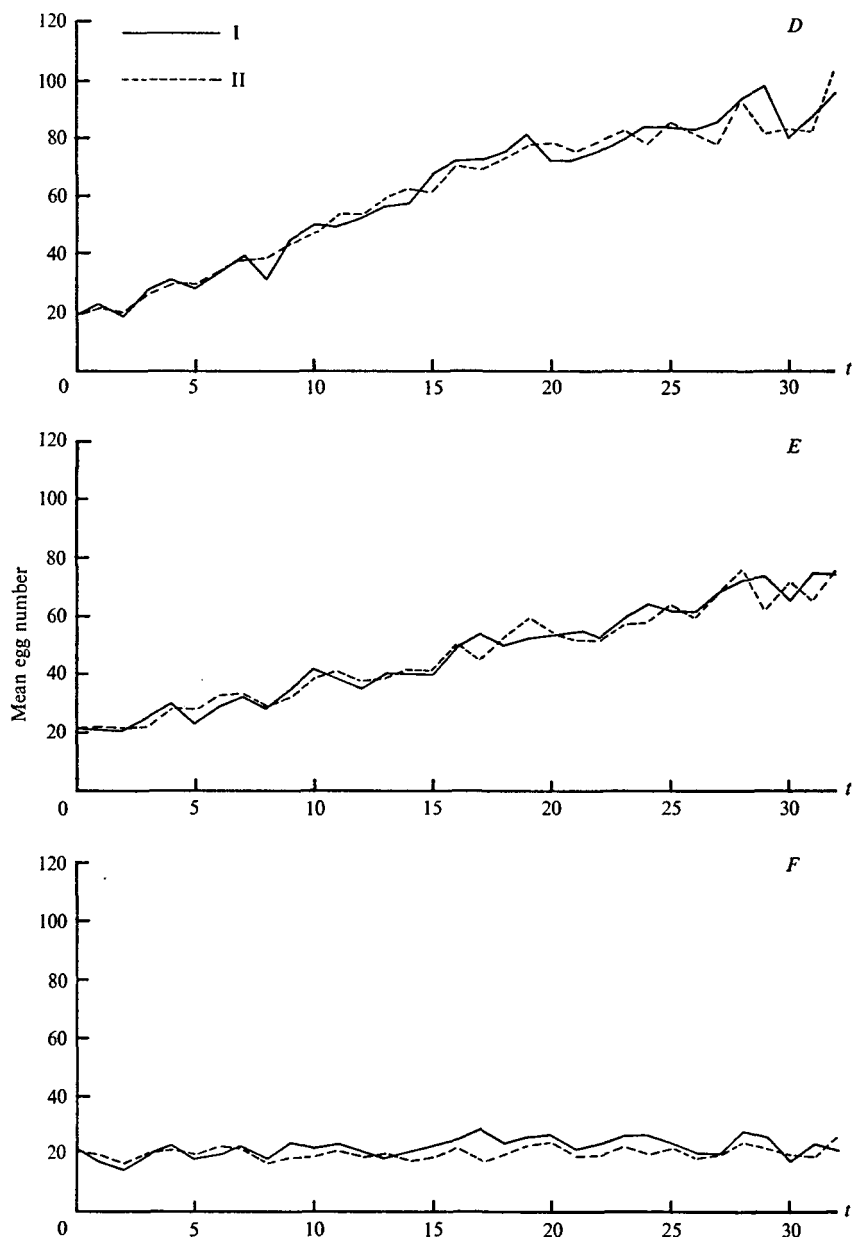
Fig. 2. Scores on D, E and F replicates.

Full-sister heritability estimates plotted against generation number are presented in Fig. 5 for each of the five set of lines (replicates pooled). No overall changes in heritability during the selection processes were detected, as shown in Table 3. Daughter–dam estimates gave a similar result but their pattern of variation per generation was more erratic than that of the full-sister estimates, and only the overall pattern of change is given in Table 3.

After selection was stopped (generation 32) all lines were relaxed and kept in population cages. Unfortunately, all A and B cages were accidentally lost. After a relaxation period of seven months, samples were taken from the C–I, D–I and E–I cages. The mean egg laying and the heritabilities of these relaxed lines were estimated and the results are shown in Table 4. The effect of relaxation was calculated
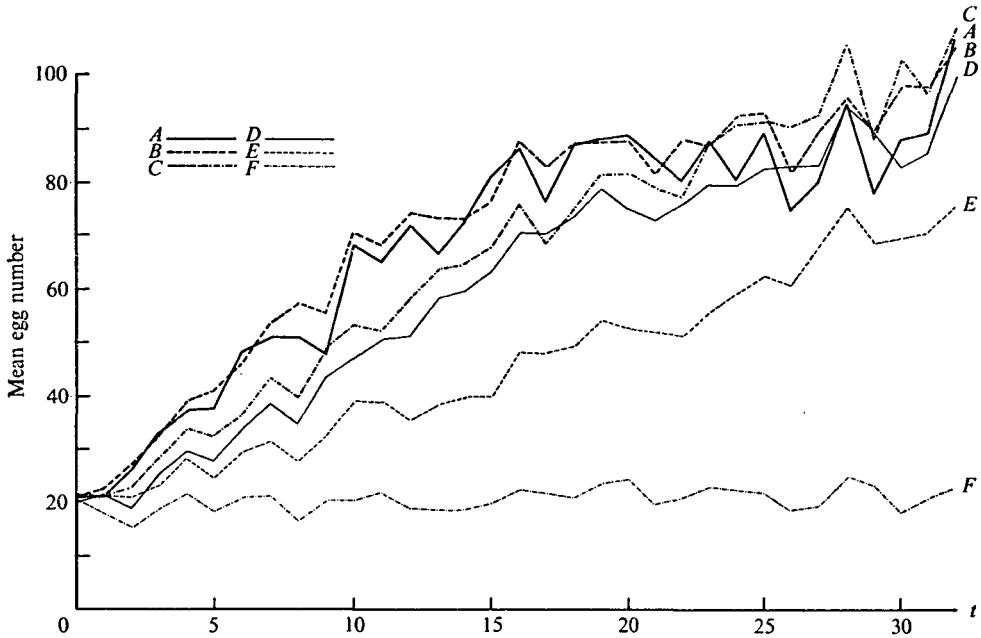

Fig. 3. Scores on the selected lines (replicates pooled).

as the difference between the performance of the line in the last generation of selection and its performance after the relaxation period. The heritabilities were estimated by daughter–dam regression using a design including divergent selection in the mothers to increase the statistical precision of the estimate (Hill, 1970). A significant relaxation effect was found in the C–I and D–I lines, the effect corresponding to C–I, the line showing the greatest response to selection, being largest. The heritability estimates were considerably lower than those estimated by full-sister correlation shown in Fig. 5 and in the case of the D–I line the estimate was not significantly different from zero.

(iii) *Predicted and realized response to selection*

When considering the responses to selection, it was found convenient to divide the experiment into two periods (generations 0–16, 16–32). The first period was characterized by a pronounced and regular response which was very attenuated in the second period except in line E. The selection differentials applied and the predicted and observed responses to selection are given in Table 5 for the two periods considered. The predicted response to selection per generation was evalu-
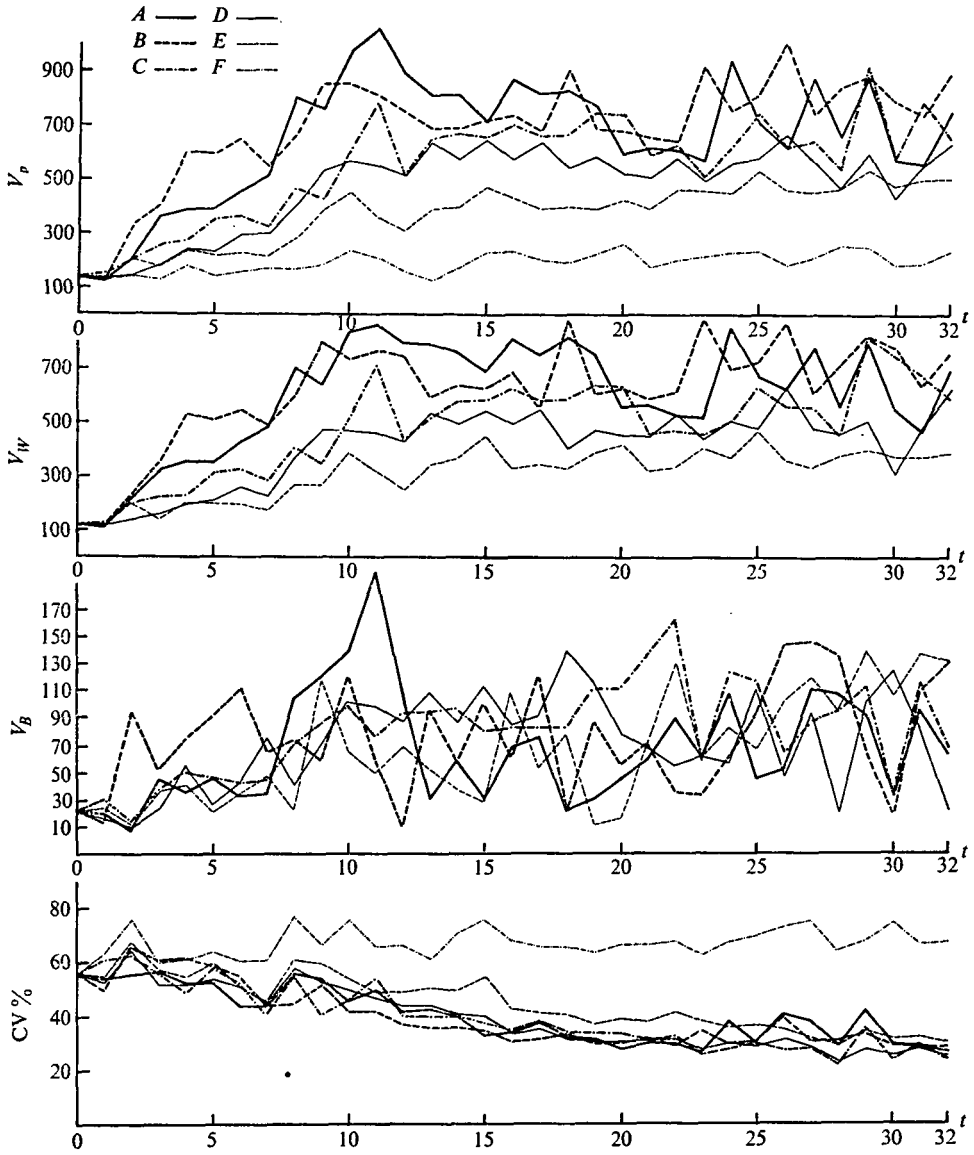
Fig. 4. Between-family (V_B), within family (V_W) and total phenotypic (V_p) variances and coefficients of variation (CV) of selected lines (replicates pooled).

ated as the product of the heritability estimated by daughter–dam regression in the base population and the corresponding selection differential. The observed response was calculated by substraction every generation. The theoretical intensities of selection were not achieved and a small but consistent reduction was observed in all lines. This reduction was more marked at higher selection intensities and in the second period as compared to the first. Predicted and observed responses to selection were in good agreement during the first 16 generations of selection, but the prediction deteriorated during the last 16 generations of selection.
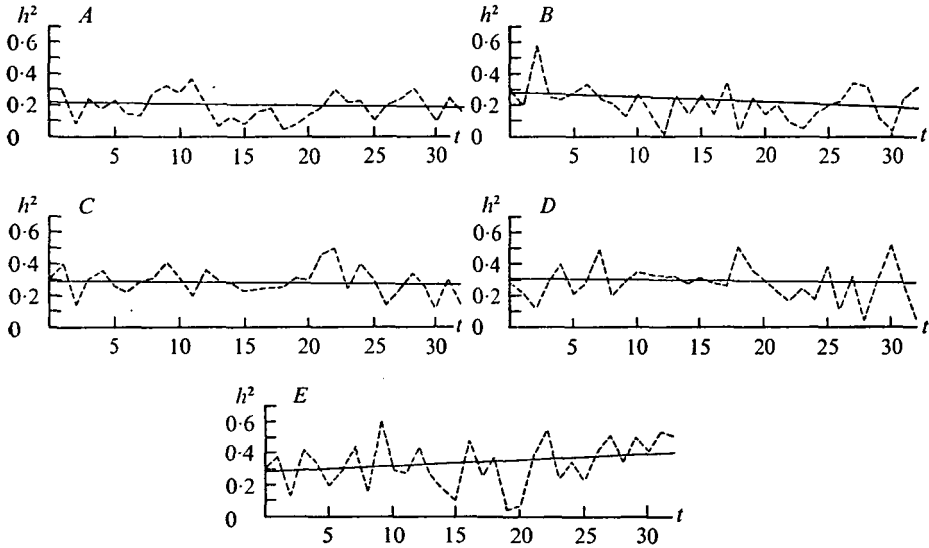
Fig. 5. Linear regressions of heritability estimates from full-sister correlation analysis on generation number (replicates pooled).

Table 3. *Linear regression coefficients of heritability estimates on generation number* (*replicates pooled*)

Line	Full-sister correlation estimates	Daughter–dam regression estimates
A	$-0{\cdot}0009 \pm 0{\cdot}0014$	$-0{\cdot}010 \pm 0{\cdot}020$
B	$-0{\cdot}0027 \pm 0{\cdot}0017$	$-0{\cdot}030 \pm 0{\cdot}010$**
C	$-0{\cdot}0001 \pm 0{\cdot}0014$	$-0{\cdot}005 \pm 0{\cdot}100$
D	$-0{\cdot}0012 \pm 0{\cdot}0020$	$-0{\cdot}010 \pm 0{\cdot}004$*
E	$0{\cdot}0050 \pm 0{\cdot}0026$	$0{\cdot}003 \pm 0{\cdot}003$
F	—	$0{\cdot}002 \pm 0{\cdot}002$

$* \ P < 0{\cdot}05; \quad ** \ P < 0{\cdot}01.$

Table 4. *Effect of relaxed selection on performance and the heritabilities of the relaxed lines with standard errors*

(The final mean is that value ultimately reached by the selected line.)

Line	Relaxation effect	Final mean	$h^2 \pm$ S.E. (h^2)
C-I	20·70**	104·98	$0{\cdot}10* \pm 0{\cdot}05$
D-I	5·25**	96·61	$0{\cdot}07 \pm 0{\cdot}04$
E-I	3·06	74·87	$0{\cdot}17** \pm 0{\cdot}04$

$* \ P < 0{\cdot}05; \quad ** \ P < 0{\cdot}01.$

Table 5. *Selection differentials (i) and their standardized values ($\bar{\imath}$) applied to the lines; predicted (R_p) and observed (R_0) responses to selection*

(Average values taken over generation periods for the pool of the two replicates).

Lines (theoretical standardized selection differential)	Generation period	i	$\bar{\imath}$	R_p	R_0
A ($\bar{\imath} = 1 \cdot 02$)	0–16	19·26	0·85	5·20	4·07
	16–32	19·17	0·71	5·17	1·31
	0–32	19·22	0·78	5·19	2·69
B ($\bar{\imath} = 0 \cdot 87$)	0–16	18·47	0·80	4·99	4·13
	16–32	18·36	0·66	4·96	1·14
	0–32	18·41	0·73	4·97	2·64
C ($\bar{\imath} = 0 \cdot 70$)	0–16	13·04	0·65	3·52	3·43
	16–32	13·85	0·54	3·74	2·07
	0–32	13·44	0·60	3·63	2·75
D ($\bar{\imath} = 0 \cdot 54$)	0–16	9·57	0·51	2·58	3·16
	16–32	11·03	0·47	2·98	1·87
	0–32	10·30	0·49	2·78	2·51
E ($\bar{\imath} = 0 \cdot 40$)	0–16	5·99	0·36	1·62	1·66
	16–32	7·91	0·37	2·13	1·71
	0–32	6·95	0·37	1·88	1·69
F ($\bar{\imath} = 0$)	0–16	0·02	0·0006	0·005	0·13
	16–32	0·03	0·0011	0·008	0·02
	0–32	0·02	0·0009	0·005	0·07

Table 6. *Inbreeding coefficients after 32 generations of selection (replicates pooled)*

Line	A	B	C	D	E	F
F	0·57	0·36	0·23	0·11	0·06	0·02

Inbreeding coefficients were calculated from pedigrees in all replicates and the pooled results after 32 generations of selection are shown in Table 6.

4. DISCUSSION

Considering the selection results first, it was found convenient to divide the experiment into two periods (generations 0–16, 16–32). The responses achieved during the first period were practically linear and they were in good agreement with the predictions. Using a deterministic model, this agreement was not unexpected as 16 generations of selection in only one sex are equivalent in terms of response to individual selection, to eight generations of selection for a trait measurable on both sexes and well within the range of usefulness of prediction usually found in selection experiments (Clayton, Morris & Robertson, 1957; Gall, 1971). During the second period prediction deteriorated in all lines, this deterioration being greatest in lines A and B which were the ones selected at the highest intensities and at smallest

population sizes. By the end of the experiment (generation 32), the rate of response to selection had been strongly reduced in all but the E lines and some of the lines, particularly A and B, seemed to be reaching a plateau. Although the magnitude of the heritability estimates has been maintained throughout the experiment, a non-significant reduction was present in all but the E lines at later selection stages. Furthermore, when the heritabilities were estimated at the end of the experiment by an appropriate design, rather than by using the selection data based on a small number of families, a marked decrease in the magnitude of the heritability of the selected lines was found. A progressive reduction of the additive variance can then be associated with the observed attenuation of the selection response.

Opposing natural selection reduced the selection differentials through deaths and reproductive failures among the selected individuals. This phenomenon has been observed in all lines but it was considerably more pronounced in those lines selected at smaller population sizes and/or when selection progressed. Although all selected lines except E showed a similar final performance, the reduction of the selection differentials was much more marked in the A and B lines than in the other lines. The effect of relaxation was also greatest in the lines attaining higher performances. It may then be concluded that natural selection opposed artificial selection because of the level of inbreeding attained by the most strongly selected lines.

When considering optimal selection strategies the results can be more conveniently examined however by taking generation 25 as the dividing point. In a model where the selected trait is controlled by a large number of unlinked loci each with small effect, the proportion selected every generation from T scored individuals to give maximum final response in t generations of selection has been shown by Robertson (1970) to be a function of t/T. In this experiment,

$$t/T = 25/200 = 1/8,$$

corresponds to an optimum selected proportion of approximately 10 % (Robertson, 1970, Fig. 1). This is in agreement with our result of the B lines, selected at 10 %, which ranked first from generation 20 to generation 25. Similarly,

$$t/T = 32/200 = 4/25$$

corresponds in Robertson's graph to selected proportions between 10 and 20 %, and is also consistent with the result of the C lines showing the highest performance from generation 25 onwards. The theory is also in accordance with highest intensities of selection leading to the largest short-term gains (A and B lines selected at 5 and 10 %).

In a commercial breeding programme, maximizing final selection gains may not be an attractive strategy for the breeder as those gains will be more heavily discounted than initial gains. Therefore, the profitability of such an enterprise will have to be evaluated (James, 1972) as high selection intensities may lead to an earlier cessation of the response to selection as has in fact happened in this experiment.

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