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Correlated Response in Male and Female Sterility to Selection for Pupa Weight in *Tribolium castaneum*[1]

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Summary. The correlated responses in male and female sterility to 50 generations of individual selection for pupa weight in *Tribolium* were analyzed. Two replicate lines (S-lines) were selected for heavier pupa weight and stabilizing selection for pupa weight was practiced in two replicate control lines (C-lines). There was close agreement between replicates in both sets of lines for direct and correlated responses. The rate of inbreeding has been constant for all lines (approximately 0.5% per generation).

Regression of generation means for pupa weight on generation of selection indicated a significant linear regression in the direct response for both lines. The linear increases of 46 and 55 μg. per generation in the S-lines accounted for 98% of the variation among generations and the linear decreases of 5 and 10 μg. per generation in the C-lines accounted for 70–90% of the variation in the generation means.

Maximum likelihood estimators were used to calculate the frequency of male and female sterility for each generation and line. Average sterility in the base population ranged from about 4 to 12% for both sexes. Polynomial regressions of percent sterility on generation of selection showed that quadratic and higher order regressions were occasionally significant but accounted for a relatively small fraction of the total variation. In the two S-line replicates, linear regression coefficients of percent sterility on generation number were $0.16 \pm .09$ and $0.20 \pm .07$ for males and $0.72 \pm .08$ and $0.54 \pm .08$ for females, suggesting a larger correlated response in female than in male sterility. In the C-lines, linear regression coefficients were $0.02 \pm .08$ and $-.12 \pm .05$ for males in the two replicates and $-.05 \pm .05$ and $-.05 \pm .05$ for females. Estimates of realized genetic correlations between pupa weight and sterility in the S-lines ranged from 0.04 to 0.14 for males and from 0.14 to 0.37 for females when the heritability of sterility was allowed to take on values from 0.05 to 0.25.

Introduction

Most experimental results have shown that the effect of artificial selection based on a single polygenic character is multiple in the sense that correlated responses are observed in secondary characters as well as direct response in the primary one (for examples in various species see Clayton *et al.*, 1957; Dawson, 1966; Falconer, 1954 and Lerner, 1946). Correlated responses may be due to the genetic structure of the population and arise as a result of pleiotropy of gene effects, linkage and/or epistasis. As Falconer (1953) has pointed out, there are at least two types of correlated responses. There may be a direct correlated response in which the secondary character may increase or decrease, depending on the direction of selection for the primary character. Alternatively, the secondary character may decline regardless of the direction of selection for the primary character. Secondary characters which are components of fitness might respond in this manner. Lerner (1954) related this second type of correlated response to genetic homeostasis and several investigators have presented evidence of genetic homeostasis (Dawson, 1966; Hiraizumi, 1961; Latter and Robertson, 1962 and Verghese and Nordskog, 1968).

Correlated responses are of interest not only because their quantitative analyses may elucidate facts about a number of genetic parameters of populations but also because they provide information on factors which may influence the rate and limit to direct selection. If correlated responses are found to limit the direct response to selection, it would be of interest to examine ways of breaking the limit. There is evidence (Abplanalp, 1962; Falconer and King, 1953 and Roberts, 1967a, b) that apparent plateaus may be surpassed by use of appropriate methods.

The objectives of the present study were to estimate the effects of 50 generations of individual selection for pupa weight on male and female sterility. A preliminary report by Enfield (1969) indicated that sterility had increased during the first 40 generations of selection and it was of interest to determine whether males and females contributed equally to the increase.

Materials and Methods

Two highly inbred lines of *Tribolium castaneum* originating from the same synthetic stock were crossed to produce a base population for the selection experiment. Individuals of the F_3 generation were randomly assigned to four lines: two replicate select lines (*S*-lines) and two replicate control lines (*C*-lines). Replicates were "time" replicates in the sense that one followed the other by two weeks.

In each generation and line 36 males and 72 females were selected as parents for the next generation. Each

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male was mated at random with two females with the restriction that full-sib matings were avoided. Individuals were mated at a constant age which was about 10 days subsequent to sexual maturity. The selection criterion was 21-day pupa weight and selection was on an intra-half-sib family basis. The heaviest male and two heaviest females from each half-sib family were selected in the *S*-lines and the male and two females nearest the half-sib family mean for each sex were selected from each half-sib family in the *C*-lines (stabilizing selection).

On the 21st day following the middle day of a three-day egg-laying period the number of larvae and pupae from each female were counted. If no pupae or larvae were present the particular mating was classified as sterile. A more complete description of the experimental procedures has been given by Enfield *et al.* (1966).

It is not possible to classify individuals as sterile with complete accuracy since a given sterile mating may be the result of a sterile male, a sterile female or both. However, it is possible to estimate the frequency of male and female sterility separately for each generation and line. Table 1 shows how the estimators for male and female sterility were derived. Since mating was at random (the only known deviation from randomness was the avoidance of full-sib matings) the frequency of each type of mating is the product of the individual frequencies for fertility and sterility. It is implicitly assumed that the fertility of an individual is not affected by the fertility of its mate (i.e., no interaction between male fertility and female fertility). Equations (1) and (2) are easily derived from the frequencies of the matings of type A and B and simultaneous solution of (1) and (2) yields the estimators for the frequency of male and female sterility. It is noteworthy that the same estimators are obtained by the method of maximum likelihood.

Table 1. *Calculation of Male and Female Sterility*

Males	Females		
	$Fq\ Fq$	$Fq\ f_{(1-q)}$	$f_{(1-q)}\ f_{(1-q)}$
F_p	$p\,q^2$	$2\,p\,q\,(1-q)$	$p\,(1-q)^2$
$f_{(1-p)}$	$(1-p)\,q^2$	$2\,(1-p)\,(1-q)\,q$	$(1-p)\,(1-q)^2$

Where: F_p = fertile males with frequency p
$f_{(1-p)}$ = sterile males with frequency $(1-p)$
F_q = fertile females with frequency q
$f_{(1-q)}$ = sterile females with frequency $(1-q)$

Let: X = number of males mated to two females
A = number of matings where both females produced progeny
B = number of matings where one female failed to produce progeny
C = number of matings where both females failed to produce progeny

Then: $A = p\,q^2\,X$ (1)

$B = 2\,p\,q\,(1-q)\,X$ (2)

Solving (1) and (2):

$(1-q) = B/(2\,A + B)$ = female sterility

$(1-p) = (1/X)\,(C - B^2/4\,A)$ = male sterility

Male sterility may be due to non-functional sperm and/or of a mechanical nature resulting in failure of the sperm to be deposited. Female sterility, as estimated from these data, may be of a mechanical nature resulting in failure of the eggs to be laid but may also include egg mortality. This results from the fact that only pupae and larvae were detected by the method used to separate flour from 21-day-old progeny. In those cases where there was complete egg mortality the mating would be classified as sterile since the undeveloped eggs could not be detected.

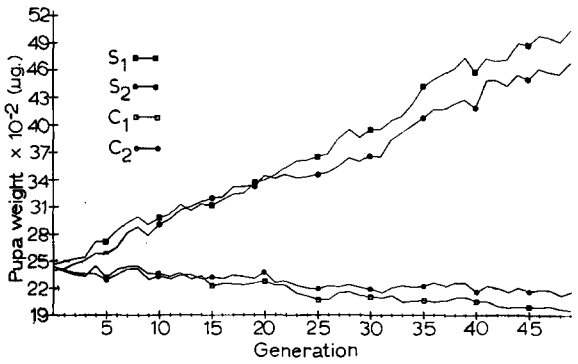

Fig. 1. Direct response to selection. Unweighted means of male and female pupa weight plotted against generation of selection for each line (*S* and *C*) and replicate (1 and 2)

Results and Discussion

A manuscript is in preparation which gives the results of a detailed analysis of the direct response to selection during the first 50 generations of selection. The direct response in pupa weight is briefly discussed in the present paper to lay the foundation for presenting the analyses of the correlated responses in male and female sterility.

The direct response to selection during the first 50 generations of selection is shown in Fig. 1 for each line and replicate. The pupa weight means for each generation are unweighted means of male and female means. There was a high degree of consistency between replicates for both lines. Linear regression coefficients of the S-line generation means on generation of selection were 55 and 46 µg. for the first and second replicates, which accounted for 98% of the variation in generation means. Hence, response to selection for greater pupa weight has been essentially linear and there was no indication of the lines approaching a plateau.

The linear regression coefficients of the C-line pupa weight means on generation of selection were negative (−5 and −10 µg.) and significant ($P < .01$) and accounted for 70—90% of the variation. The original intent was for the C-lines to serve as controls for the *S*-lines. If the decline in pupa weight of the *C*-lines was due to environmental time trends or inbreeding depression (the rate of inbreeding was approximately 0.5% per generation for all lines) the *C*-lines would be unbiased controls (assuming no genetic-environmental interaction). A replica of the original base population was established from the two original inbred lines at generation 28 and two replicate lines (R-lines) were maintained by random selection and random mating through generation 50. The results from the R-lines indicated that neither environmental time trends nor inbreeding depression had an effect on

pupa weight and suggested that the decline in pupa weight of the C-lines was a result of the stabilizing selection, thereby showing the C-lines to be inappropriate controls. Though not significant, Bray *et al.* (1962) also observed a decline in pupa weight of *Tribolium* lines subjected to stabilizing selection for pupa weight over 8 generations. Since it was not the purpose of this paper to examine the effects of stabilizing selection, it is sufficient to note that the absolute values for male and female sterility of each line were subjected to analysis. The differences between lines ($S_1 - C_1$ and $S_2 - C_2$) were also analyzed, but, as the results show, the added precision was negligible.

Table 2. *Mean % Sterility by Groups of Generations for Each Line* and Sex*

Gen.	S_1	S_2	C_1	C_2
Males				
0– 9	4.19 ± 1.37	4.81 ± 1.43	8.94 ± 1.73	6.75 ± 1.90
10–19	2.38 ± 0.58	6.65 ± 2.46	17.22 ± 1.80	8.95 ± 1.56
20–29	4.05 ± 2.25	10.39 ± 1.84	19.33 ± 3.34	6.63 ± 2.00
30–39	10.58 ± 3.01	13.56 ± 2.88	16.66 ± 1.80	3.39 ± 1.39
40–49	8.51 ± 5.49	10.01 ± 2.28	9.32 ± 1.75	3.11 ± 1.18
0–49	5.94 ± 1.38	9.08 ± 1.05	14.29 ± 1.12	5.77 ± 0.77
Females				
0– 9	4.25 ± 1.37	6.67 ± 1.05	12.35 ± 1.74	9.73 ± 1.78
10–19	2.79 ± 0.56	9.80 ± 1.33	9.79 ± 1.67	11.80 ± 1.53
20–29	6.21 ± 2.28	24.15 ± 2.30	13.55 ± 1.63	10.60 ± 1.06
30–39	12.62 ± 2.75	22.42 ± 2.78	8.54 ± 0.92	8.02 ± 1.55
40–49	34.24 ± 4.95	28.49 ± 3.46	10.57 ± 1.26	9.71 ± 1.28
0–49	20.58 ± 1.87	18.30 ± 1.58	10.96 ± 0.68	9.97 ± 0.65

* S = select lines, C = control lines (stabilizing selection) and replicates are designated by the subscripts 1 and 2.

Table 2 gives the mean percent sterility by groups of 10 generations for each line, replicate and sex. If it is assumed that the mean values during the first 10 generations of the experiment are representative of those in the base population, the means indicate that sterility of the foundation stock ranged from 4 to 12%. There was a tendency for sterility to be lower for the S-lines than for the C-lines during the early generations of selection. This could have been caused by a negative environmental correlation between weight and sterility. Perhaps the heavier individuals selected for parents of the next generation in the S-lines were heavier, in part, because of favorable environmental effects which also favored lower sterility. The means for percent sterility suggested some trends during the 50 generations of selection, but these will be more fully examined by subsequent analyses.

Table 3. *Analyses of Variance for Male and Female % Sterility*

Source	d. f.	Male M.S.	Female M.S.
Line (L)	1	317.5	4029.4*
Rep. (R)	1	362.6*	133.1*
Gen. (G)	49	69.0*	138.5**
$L \times R$	1	1701.0**	20.8
$L \times G$	49	71.1	133.2**
$R \times G$	49	42.7	42.2
$L \times R \times G$	49	59.8	30.4

* $P < .05$
** $P < .01$

The analyses of variance for male and female percent sterility are separately presented in Table 3. Line and generation were considered as fixed and replicate as a random source of variation. Exact tests of significance were available for the line (L), generation (G) and $L \times G$ interaction sources of variation. Approximate tests of significance were made for the replicate (R), $L \times R$ interaction and $R \times G$ interaction sources of variation by assuming that σ^2_{LRG} was negligible (i.e., the expected mean square for the $L \times R \times G$ interaction source of variation is $\sigma^2 + \sigma^2_{LRG}$, but if it can be assumed that $\sigma^2_{LRG} = 0$, then the mean square for the $L \times R \times G$ interaction estimates the within line, replicate and generation variance). The line source of variation was significant ($P < .05$) for females only, indicating that the correlated effect of selection which differentiated the lines for percent sterility was more important for females. Replicate and generation were significant ($P < .05$) sources of variation for both sexes. The direction of the significant differences for the main effects and the origin of the two significant ($P < .01$) interactions ($L \times R$ for males and $L \times G$ for females) will become evident in the following regression analyses.

Polynomial regression analyses of male and female percent sterility on generation of selection were done for the 50 generations of selection. Table 4 presents the polynomial regression analysis for male percent sterility and shows the linear, quadratic and cubic partial regression coefficients and the cumulative R^2 values. The consistency between replicates was good. The partial regression coefficients were occasionally significant but none of the polynomial terms accounted for large portions of the variation in male sterility.

Table 4. *Polynomial Regression of Male % Sterility on Generation of Selection*

Line	Linear		Quadratic		Cubic	
S_1	0.547[a]	(5)[b]	−.0002	(5)	−.00104	(12)
S_2	0.203**	(16)	−.0043	(17)	−.00046	(18)
C_1	−.119	(0)	−.0217**	(27)	0.00037	(28)
C_2	−.434*	(10)	−.0042	(13)	0.00084**	(26)
$S_1 - C_1$	0.667	(3)	0.0216*	(13)	−.00141*	(21)
$S_2 - C_2$	0.808**	(21)	−.0000	(21)	−.00129*	(30)

[a] Partial regression coefficient
[b] Cumulative R^2 values × 100 are in parentheses
* $P < .05$
** $P < .01$

Table 5. *Polynomial Regression of Female % Sterility on Generation of Selection*

Line	Linear		Quadratic		Cubic		Quartic	
S_1	0.685**[a]	(62)[b]	−.0622	(63)	0.00008	(63)	0.00012**	(70)
S_2	0.462**	(49)	−.0602	(49)	0.00020	(49)	0.00011**	(57)
C_1	−.025	(2)	0.0007	(2)	−.00007	(3)		
C_2	−.112	(2)	0.0008	(3)	0.00017	(3)		
S_1-C_1	0.710**	(69)	−.0304	(69)	0.00015	(69)	0.00006	(70)
S_2-C_2	0.574**	(50)	−.0528	(51)	0.00003	(51)	0.00009*	(56)

[a] Partial regression coefficient
[b] Cumulative R^2 values × 100 are in parentheses

* $P < .05$
** $P < .01$

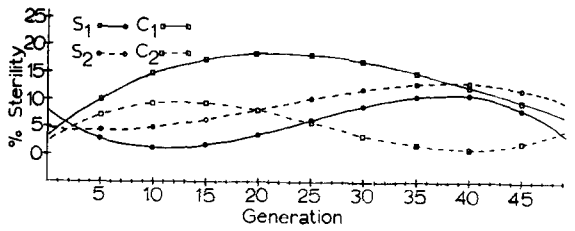

Fig. 2. Correlated response in male sterility. Cubic polynomial regression curves of male percent sterility on generation of selection

The analyses of the differences between lines ($S_1 - C_1$ and $S_2 - C_2$) did not yield appreciably larger R^2 values and suggested that the within generation deviations from the regression curve of male sterility in the *S*-lines were no more accurately predicted by the deviations from the regression in the *C*-lines than from the means of the *S*-lines themselves.

The cubic polynomial regression curves shown in Fig. 2 graphically illustrate the correlated response of male sterility to selection for pupa weight. The correlated response was small or negligible in all lines. However, the close correspondence between the *S*-line replicates suggested that the slight increase observed for the *S*-lines may be a real correlated response. The origin of the significant line x replicate interaction observed in Table 3 is illustrated by Fig. 2. The difference between replicates was small in the *S*-lines and larger in the *C*-lines.

Table 5 gives the polynomial regression analysis for female percent sterility for the 50 generations of selection. The partial regression coefficients for each polynomial term and the cumulative R^2 values are shown. There was a high degree of consistency between replicates for both lines. In the *S*-lines, the linear partial regression coefficients were positive, significant ($P < 0.1$) and accounted for 50−60% of the variation. The quadratic and cubic terms were unimportant sources of variation, but the quartic terms were significant ($P < .01$) and increased the cumulative R^2 values to 60−70%. In the *C*-lines, none of the polynomial terms was a significant source of variation and the maximum cumulative R^2 value was 3%. As in the male data, analyses of the differences between lines added little precision to the results.

The correlated response of female sterility to selection for pupa weight is illustrated in Fig. 3 by the polynomial regression curves of female percent sterility on generation of selection. In the *C*-lines, there was little change in female sterility during the course of selection. In the *S*-lines, the correlated response to selection was an obvious increase in female sterility. The deviation from linearity of the correlated response in the *S*-lines was likely due to environmental effects since the linear regression accounted for the majority of the variation. However, the initial decrease could have been due to a negative environmental correlation between pupa weight and sterility. Those individuals selected for parents of the next generation may have been healthier and more vigorous, which could have caused them to be jointly heavier and less likely to be sterile. A positive genetic correlation would eventually override this effect and cause sterility to increase. This points to the danger in interpreting correlated responses observed over short periods of time. The apparent plateau of the correlated response in female sterility between generations 25 and 40 is difficult to explain. It is unlikely to be due to rare events such as a mutation of a major gene or recombination since it occurred at the same time in both replicates.

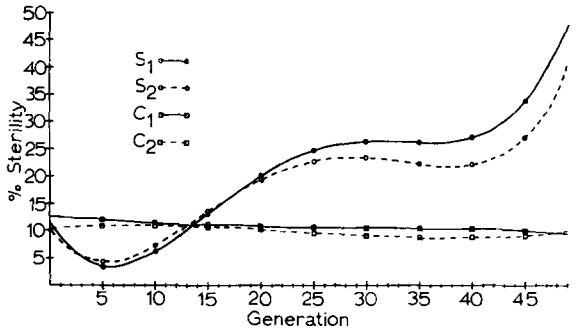

Fig. 3. Correlated response in female sterility. Polynomial regression curves of female percent sterility on generation of selection are quartic for *S*-lines and cubic for *C*-lines

Table 6 summarizes the correlated responses in male and female percent sterility to selection for pupa weight. Regression coefficients from the linear regression of sterility on generation of selection are shown. In contrast with the preceding discussion, this implicitly assumes that the correlated responses were essentially linear. All of the linear regression coefficients were positive for the *S*-lines. Those for the females were significant ($P < .01$) and approximately three times as large as those for the males, indicating a more pronounced correlated response in female than in male sterility. If sterility continues at the rate dictated by the linear regression coeffi-

Table 6. *Linear Regression of % Sterility on Generation of Selection*

Line	Male	Female
S_1	0.157 ± .094	0.717 ± .080
S_2	0.203 ± .068	0.535 ± .079
C_1	0.020 ± .078	−.051 ± .047
C_2	−.120 ± .051	−.049 ± .045
S_1-C_1	0.137 ± .122	0.767 ± .075
S_2-C_2	0.323 ± .091	0.585 ± .084

cients, it is predicted that sterility will eventually limit the direct response to selection.

These results from the *S*-lines could be explained either in terms of a positive genetic correlation between pupa weight and sterility, regardless of the direction of selection, or in terms of genetic homeostasis where the sign of the realized genetic correlation between the selected metric trait and the component of fitness would depend on the direction of selection from some intermediate optimum. Since selection for pupa weight was not practiced in the downward direction this question can not be resolved for these data. However, the results from the *C*-lines offer some indirect evidence. Table 6 shows that the linear regressions of sterility on generation of selection tended to be negative but seldom significant for both sexes in the *C*-lines. On the surface, these results suggest a positive genetic correlation since pupa weight also declined in the *C*-lines and argue against the homeostatic model. The issue must remain clouded, however, because direct selection for lower pupa weight was not practiced in the *C*-lines. The corresponding decreases in pupa weight and sterility observed for the *C*-lines were the result of stabilizing selection, which is not well understood.

Falconer (1960a) gave formula (1) shown in Table 7, which describes the expected correlated response in a secondary character as a result of its genetic correlation with the primary character. Rearranging formula (1) and setting the correlated response in sterility and the direct response in pupa weight equal to the linear regressions of sterility (b_{sg}) and pupa weight (b_{pg}) on generation of selection, respectively, leads to formula (2). The only value in the right side of formula (2) for which there was no estimate was h_s. By letting h_s^2 vary from 0.05 to 0.25, it was possible to make corresponding estimates for the realized genetic correlation between sterility and pupa weight. This seemed to be a reasonable range of values based on heritabilities in the literature for most fitness parameters. This method assumes that the heritabilities of sterility and pupa weight and the genetic correlation between them did not change during the course of selection. There is evidence that the heritability of pupa weight did not change significantly in these data (Enfield — manuscript in preparation), but the poor agreement between predicted and observed correlated response during later generations

Table 7. *Realized Genetic Correlation between Sterility and Pupa Weight*

$$CR_s = i\, h_p\, h_s\, r_G\, \sigma_s{}^a \quad (1)$$

$$r_G = (1/h_s)\ (b_{sg}\ \sigma_p\ h_p/b_{pg}\ \sigma_s)^b \quad (2)$$

	h_s^2				
Line	.05	.10	.15	.20	.25
			Males		
S_1	.08	.06	.05	.04	.04
S_2	.14	.10	.08	.07	.06
			Females		
S_1	.37	.26	.22	.19	.17
S_2	.32	.22	.18	.16	.14

[a] Subscripts s and p refer to sterility and pupa weight, respectively, CR = correlated response, i = selection intensity, h = square root of heritability, r_G = genetic correlation and σ = phenotypic standard deviation

[b] b_{sg} and b_{pg} are linear regressions of sterility and pupa weight, respectively, on generation of selection

of selection as demonstrated by Falconer (1960b) and the theoretical results of Bohren *et al.* (1966) may make the assumption of no change in the genetic correlation subject to debate. Estimates of the realized genetic correlation between pupa weight and sterility are shown in Table 7 and were calculated for the *S*-lines only. The realized genetic correlations ranged from 0.04 to 0.14 for the males and from 0.14 to 0.37 for the females.

Several other investigators have reported correlated responses in sterility which were primarily due to females. Reports by Clayton and Robertson (1957) and Clayton *et al.* (1957) on a long-term selection experiment with *Drosophila* showed that selection for abdominal bristle number resulted in declines in fertility which were larger in low than in high lines. One high line was lost because of female infertility and all low lines required intermittent relaxation of selection to save them from extinction. Extreme females of the low lines tended to be infertile. Dawson (1965, 1966) selected for fast and slow developmental rate in *Tribolium* and productivity declined so rapidly in the slow lines that the selection procedure had to be modified after 5 generations. It was determined that male fertility had not decreased and that the correlated response was due to a reduction in egg hatchability and larval survival. Note that female sterility of the present study includes egg mortality. Latter (1966), in a line of *Drosophila* selected for scutellar bristle number, observed an increase in the incidence of sterility. Outcrosses indicated that females only had increased in sterility. Latter and Robertson (1962) noted that in the later generations of a low line of *Drosophila* selected for wing length the egg laying ability of females was reduced and that male fertility was apparently not greatly affected. Lerner and Dempster (1951) showed that the decrease in realized selection differentials observed during

selection for shank length in poultry was not due to males.

There are also studies which have shown correlated responses in male fertility. Fowler and Edwards (1960) analyzed strains of mice previously selected for large and small body size and observed that the percent of sterile pair matings was greater in the select lines than in the control. Outcrosses revealed that females of the small line but that males of the large line were responsible for the increased sterility. In lines of *Drosophila* subjected to rapid inbreeding and selected for rate of development, Hollingsworth and Smith (1955) ascribed the declines in egg hatchability to be largely caused by infertility of males.

Other investigations which have not separated correlated responses into their component male and female parts have varied in their results. Selection over long periods of time has generally been accompanied by a reduction in reproductive fitness but some studies (Brown and Bell, 1961; Dempster *et al.*, 1952 and Yamada *et al.*, 1958) have shown that observed plateaus or decreased responses to selection were not due to decreases in reproductive fitness or, in some cases, components of reproductive fitness.

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