

SEX AND SELECTION FOR A QUANTITATIVE CHARACTER IN *DROSOPHILA*

I. SINGLE-SEX SELECTION

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Summary

Selection for abdominal bristle number was done in six lines, three with selection in females only and three in males only. Selection was equally effective (for a given selection differential) when carried out in either sex, even though more than one-third of the additive genetic variation was sex linked. Most response in a given sex was found in the treatment selected in that sex. Relaxed lines failed to show fluctuating scores in the two sexes as predicted by Griffing (1965). Epistatic decay may have masked these effects.

Formulae to predict response to selection, when there is a scale difference between the sexes and the genetic correlation between sexes is less than unity, are presented. Predictions of the relative response in males and females from these formulae were in good agreement with observed response in the single-sex abdominal bristle selection lines and in the abdominal bristle selection lines of Jones, Frankham, and Barker (1968).

I. INTRODUCTION

Although the selection intensity is generally much greater in males than females in animal breeding, there is little experimental evidence on the effects of such differential selection. Beilharz (1960) suggested that, where sex-linkage operates, rate of genetic progress under selection will be highest when the most intense selection is practised in the homogametic sex. Griffing (1965) also suggested that selection may not be equally effective in both sexes when sex-linkage is present. However, Harrison (1953) found that selection was equally effective in the two sexes. His study was done on a limited scale, and only excludes the possibility of a gross difference in the effectiveness of selection in either sex. Further, information concerning the importance of sex-linked effects was not provided.

Griffing (1966*a*) showed that the response to identical selection pressure may be different for the two sexes when autosomal genes have different effects in the two sexes and in this case suggested that selection may be more efficient in one sex than the other. In a further paper Griffing (1966*b*) considered the joint effects of sex-linked and sex-influenced inheritance on the response to selection in the two sexes and also considered the problem of distinguishing between these two effects. Rahnefeld *et al.*

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(1963) suggested that an incomplete genetic correlation between performance in the two sexes ($r_{Gmf} < 1.0$) may have been responsible for a lower realized than estimated heritability in selection for body weight in mice. Horton and McBride (1964) demonstrated that the relative response in males and females for body weight in poultry was changed with different relative selection intensities in the two sexes. This was apparently due to an incomplete genetic correlation between performance in the two sexes.

As genotype \times sex interaction effects (whether due to sex-linked or sex-influenced inheritance) have been found to be of importance for economically important characters (e.g. Knapp and Phillips 1942; Comstock, Winters, and Cummings 1944; Shaklee, Knox, and Marsden 1952; Beilharz 1963; Horton and McBride 1964), an attempt is made to evaluate the effect of these in selection schemes for quantitative characters. In this study the effects of selection in females only and in males only are compared for a character partly controlled by sex-linked genes.

Sex dimorphism is found for a variety of traits in many species and in such cases scale differences between the sexes in selection response are often found (e.g. MacArthur 1949; Harrison 1953; Sheldon 1963; Jaap 1966; Park *et al.* 1966). Formulae to predict response to selection in males and females in the presence of such scale effects are presented here.

II. MATERIALS AND METHODS

The following selection lines were initiated, each with 20 pairs of randomly chosen parents, from the Canberra strain (Sheridan *et al.* 1968) of *Drosophila melanogaster*: (1) female selection only (F); and (2) male selection only (M).

For (1), three replicate lines (designated F_A, F_B, and F_C) were selected for fifth abdominal bristle number in *females* only. The selection intensity in females was 20% (20/100) per generation for the first five generations and 10% (20/200) for a further 25 generations. Twenty males were chosen at random each generation. These males were scored each generation and after generation 5 a further 20 randomly chosen males were also scored each generation.

For (2), three replicate lines (designated M_A, M_B, and M_C) were selected for fourth abdominal bristle number in *males* only. The selection intensity in males was 20% (20/100) per generation for the first five generations and 10% (20/200) for a further 25 generations. Twenty females were chosen at random each generation. These females were scored each generation and after generation 5 a further 20 randomly chosen females were also scored each generation.

Methods and culture conditions were described by Frankham, Jones, and Barker (1968*a*).

At generation 5, and every fifth generation thereafter, relaxed lines were split from each of the selection lines and scored in the first, second, and fifth generations of relaxation. Methods used in maintaining and scoring the relaxed lines were described by Frankham, Jones, and Barker (1968*b*).

III. RESULTS

(a) Response to Selection

As the lines had different selection differentials the average responses for the F and M treatments have been plotted against average cumulative selection differential (Fig. 1). Average response of the 20-pair selection lines of Jones, Frankham, and Barker (1968) (selected in both sexes at intensities of 10, 20, or 40%) have also been included (2Z) for comparison. The overall response in all three

treatments was very similar. Selection in females only tended to give relatively more response in females than males, while selection in males only gave relatively more response in males. Selection in both sexes (2Z) produced response in both sexes intermediate between F and M.

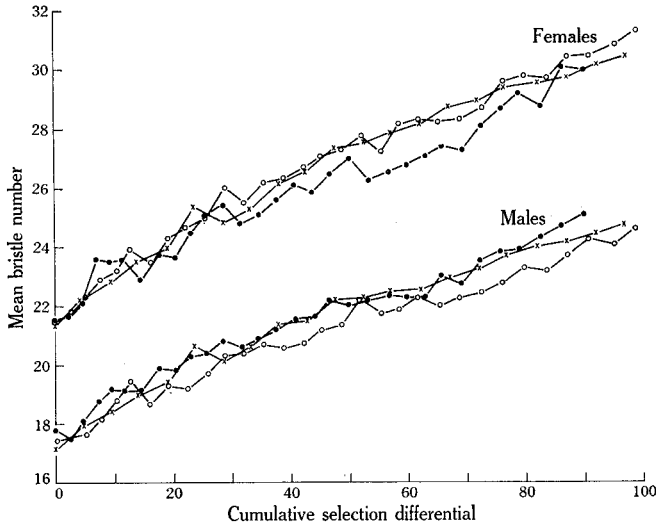


Fig. 1.—Treatment mean response of males and females to selection for abdominal bristle number in the F (○), M (●), and 2Z (×) lines plotted against average cumulative selection differential.

Responses of the individual F and M lines plotted against cumulative selection differential are shown in Figures 2 and 3. For both treatments there was considerable variation among replicates.

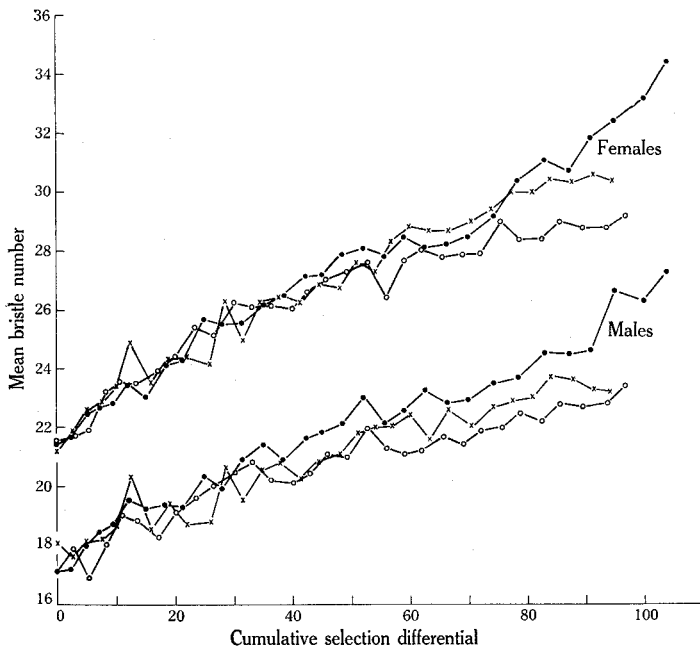


Fig. 2.—Response of males and females to selection for abdominal bristle number in the F lines plotted against cumulative selection differential. × F_A; ● F_B; ○ F_C.

Griffing (1965) showed that if response to single-sex selection was due to sex-linked genes, then on relaxation the male and female means would fluctuate due

to the equilibration of gene frequencies in the two sexes. As more than one-third of the additive genetic variation for this character was sex-linked (Sheridan *et al.* 1968) sex-dimorphism ratios (ratio of male score to female score) for the last selected generation and the first two relaxed generations for each set of relaxed lines are

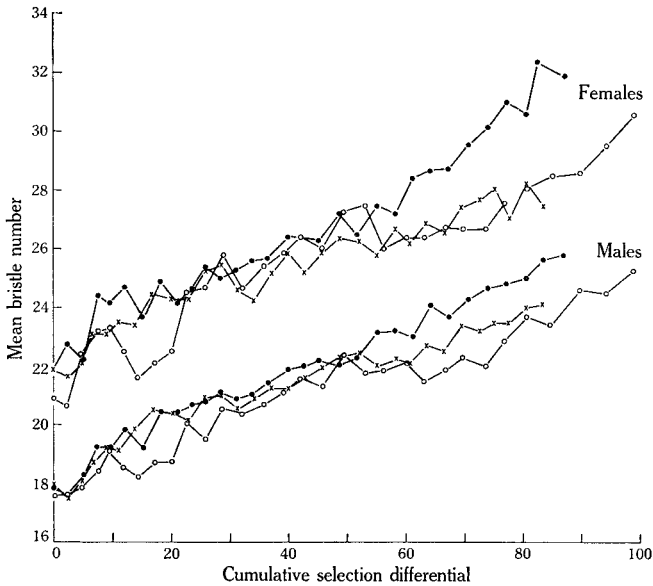


Fig. 3.—Response of males and females to selection for abdominal bristle number in the M lines plotted against cumulative selection differential. \times M_A ; \bullet M_B ; \circ M_C .

shown in Table 1. The sex-dimorphism ratio provides a convenient measure of variation in the sex dimorphism (sex difference) independent of scale effects. There was no clear evidence for the expected type of fluctuation in this ratio, *viz.* an increase followed by a decrease for the F lines, and a decrease followed by an increase in the M lines. Griffing (1965) pointed out that epistatic decay may mask such fluctuations. As important epistatic effects were present in the base population (Sheridan *et al.* 1968) this may have occurred here.

(b) *Predicting Selection Response in the Presence of Scale Effects and Incomplete Correlations between the Sexes*

To obtain estimates of the realized genetic correlation between the sexes from both the F and the M lines, it is first necessary to describe the expected response in males and females. This is complicated by a scale effect (see Fig. 1) in which females respond more than males. Response in the two sexes can be predicted as follows:

If

$$\Delta G_{m+f} = (i_m + i_f)h^2,$$

then

$$\Delta G_m = S_m(i_f + i_m)h^2,$$

and

$$\Delta G_f = S_f(i_f + i_m)h^2,$$

where ΔG is the genetic gain, i the selection differential, h^2 the heritability, S the scaling factor, and the subscripts m and f refer to males and females respectively.

The scaling factors represent the proportionate response in males (S_m) and females (S_f). In the base population S_m is estimated as the regression coefficient of

TABLE I
CHANGE IN THE SEX-DIMORPHISM RATIO ON RELAXATION FROM SELECTION IN THE F AND M LINES

Line	Relaxed Generation	Generation from which Selection was Relaxed						Average
		5	10	15	20	25	30	
F _A	0	0.814	0.785	0.778	0.775	0.764	0.763	0.779
	1	0.792	0.782	0.807	0.805	0.758	0.733	0.780
	2	0.888	0.767	0.780	0.782	0.752	0.743	0.785
F _B	0	0.822	0.781	0.802	0.828	0.790	0.790	0.802
	1	0.824	0.837	0.803	0.762	0.793	0.767	0.798
	2	0.795	0.812	0.790	0.729	0.771	0.802	0.783
F _C	0	0.806	0.780	0.779	0.755	0.792	0.802	0.786
	1	0.830	0.762	0.768	0.786	0.777	0.748	0.779
	2	0.784	0.785	0.767	0.741	0.827	0.800	0.784
M _A	0	0.811	0.828	0.816	0.852	0.852	0.875	0.839
	1	0.834	0.848	0.832	0.884	0.846	0.848	0.849
	2	0.842	0.784	0.857	0.832	0.809	0.849	0.829
M _B	0	0.797	0.820	0.831	0.843	0.823	0.808	0.820
	1	0.753	0.864	0.814	0.856	0.845	0.799	0.822
	2	0.822	0.815	0.832	0.814	0.824	0.772	0.813
M _C	0	0.823	0.789	0.817	0.840	0.831	0.828	0.821
	1	0.819	0.827	0.840	0.846	0.839	0.883	0.842
	2	0.816	0.858	0.789	0.830	0.817	0.838	0.826

male family mean on male family mean plus female family mean, i.e.

$$\begin{aligned}
 S_m &= b_{m(m+f)} \\
 &= \frac{\text{Cov}(m, m+f)}{V(m+f)} \\
 &= \frac{\text{Cov}(m, m) + \text{Cov}(m, f)}{Vm + Vf + 2\text{Cov}(m, f)} \\
 &= \frac{Vm + \text{Cov}(m, f)}{Vm + Vf + 2\text{Cov}(m, f)},
 \end{aligned}$$

where V and Cov are the total genetic variance and covariance components respectively, and m and f refer to males and females respectively.

Similarly,

$$\begin{aligned} S_f &= b_{f(m+f)} \\ &= \frac{\text{Cov}(f, m+f)}{V(m+f)} \\ &= \frac{Vf + \text{Cov}(m, f)}{Vm + Vf + 2\text{Cov}(m, f)}. \end{aligned}$$

These scaling factors are generalized to account for any symmetrical, linear scale effect between the sexes.

The values of S_m and S_f in the Canberra base population were 0.452 and 0.548 respectively from the data of experiment 1 and 0.421 and 0.579 respectively from the data of experiment 2 (averages 0.436 and 0.564 respectively) of Sheridan *et al.* (1968). These are similar to the ratios of male to male plus female abdominal bristle number and female to male plus female abdominal bristle number of 0.444 and 0.556 respectively (from Sheridan *et al.* 1968) and 0.449 and 0.551 respectively (from Frankham, Jones, and Barker 1968a) in the base population so the relation of male score to female score is a constant proportion over the whole range of abdominal bristle numbers. The sex-dimorphism ratio can then be used as a scale-independent measure of variation in abdominal bristle number. If male score/female score represents a constant proportion all data could be transformed to logarithms. In a number of cases (e.g. Butler 1952) this may be more appropriate, but for abdominal bristle number the mean and variance are unrelated (Jones, Frankham, and Barker 1968) so it does not appear to be justified.

When the genetic correlation between performance in the two sexes ($r_{G_{mf}}$) is incomplete, response can be predicted for selection in females only (F lines) as follows:

$$\begin{aligned} \Delta G_m &= S_m \cdot i_f \cdot r_{G_{mf}} \cdot h^2, \\ \Delta G_f &= S_f \cdot i_f \cdot h^2, \\ \Delta G_{m+f} &= \Delta G_m + \Delta G_f. \end{aligned}$$

For selection in males only (M lines):

$$\begin{aligned} \Delta G_m &= S_m \cdot i_m \cdot h^2, \\ \Delta G_f &= S_f \cdot i_m \cdot r_{G_{mf}} \cdot h^2, \\ \Delta G_{m+f} &= \Delta G_m + \Delta G_f. \end{aligned}$$

For selection in both sexes:

$$\begin{aligned} \Delta G_m &= S_m(i_m + r_{G_{mf}} \cdot i_f)h^2, \\ \Delta G_f &= S_f(i_f + r_{G_{mf}} \cdot i_m)h^2, \\ \Delta G_{m+f} &= \Delta G_m + \Delta G_f. \end{aligned}$$

(c) *Realized Genetic Correlations of Performance in the Two Sexes*

The realized genetic correlation can be estimated using Falconer's (1960) formula for estimating the genetic correlation from independent selection for each trait in separate lines,

$$r_{G^2} = (CR_x/R_x) \times (CR_y/R_y),$$

where R and CR represent response and correlated response to selection respectively, and the subscripts x and y refer to the two characters (two sexes here). In this case

$$r_{G_{mf}} = [(7.20/9.98) \times (8.48/7.29)]^{\frac{1}{2}} = 0.92.$$

This method gives no indication whether the realized genetic correlations from the F and the M lines were similar. Using the formulae derived in Section III(b) the realized genetic correlations between performance in the two sexes can be estimated independently from the F and the M lines as follows: from the F lines,

$$r_{G_{mf}} = (\Delta G_m / \Delta G_f) \times (S_f / S_m),$$

and from the M lines,

$$r_{G_{mf}} = (\Delta G_f / \Delta G_m) \times (S_m / S_f).$$

For abdominal bristle number $S_m = 0.436$ and $S_f = 0.564$, so the estimates from the F lines are:

$$r_{G_{mf}} = (7.20/9.98) \times (0.564/0.436) = 0.93,$$

and from the M lines,

$$r_{G_{mf}} = (8.48/7.29) \times (0.436/0.564) = 0.90.$$

Thus, the realized estimates of $r_{G_{mf}}$ from the F and the M lines were very similar.

IV. DISCUSSION

Selection here was equally effective when carried out in either sex, even though more than one-third of the additive genetic variation was sex-linked. These results contradict Beilharz's (1960) suggestion that rate of selection response would be greatest in the homogametic sex (female here) when sex-linkage is present. Griffing (1965) pointed out that the relative efficiencies of selection in the two sexes, for sex-linked loci, depends on the genetic model used to relate the monoploid genotype value of the heterogametic sex (XY) to the diploid genotypic values of the homogametic sex (XX). For selection on either sex to be equally effective overall, it must be twice as accurate for sex-linked genes (with the same effect in both sexes) on the monoploid genotype (male) as on the diploid genotype (female). Griffing (1965) showed that the selective value for a gene was linearly related to its additive effect and that the effect of male selection (for a given selection differential) on the female

mean was equal to the effect of female selection on the male mean irrespective of the relative size of the additive effects of the genes in the two sexes. As well, female selection affects the female mean in the following generation, while male selection does not affect the male mean in the following generation. Thus a simple dosage compensation effect (e.g. one dose of the X chromosome having the same effect in males as two doses in females) is not sufficient to produce the same response from selection (for sex-linked genes) in males as from selection in females (for a given selection differential), but will reduce the difference between them. Until the consequences of selection for different genetic models (relating the monoploid genotypic values in males to the diploid genotypic values in females) are derived, it is not possible to decide what type of effect is responsible for selection in either sex being equally effective, or to predict whether similar results will be obtained in mammals and birds.

Formulae to predict selection response independently in the two sexes when the genetic correlation between sexes is less than unity are presented here in a different form to those of Griffing (1966*b*) and extended to account for a scale difference between males and females in response.

A limited evaluation of predictions from these formulae can be obtained by comparing the estimated $r_{G_{mf}}$ with realized $r_{G_{mf}}$ from the single-sex selection lines and comparing the estimated scaling factors with the proportionate response in the two sexes (i.e. the realized scaling factors) in the lines of Jones, Frankham, and Barker (1968). The estimate of $r_{G_{mf}}$ in the Canberra base population was 0.78 after correction for sex-linkage biases (Sheridan *et al.* 1968). The realized values of 0.90 and 0.93 were in fair agreement with this estimate. The realized values of S_m and S_f (the proportion of the total response in males and females respectively) averaged 0.448 and 0.552 respectively for the lines of Jones, Frankham, and Barker (1968) and were similar to the base population estimates (0.436 and 0.564 respectively). It seems likely that these formulae will provide adequate predictions of selection response in males and females.

A consequence of the scale effect reported here for abdominal bristle number is that when $r_{G_{mf}}$ is less than unity, more response (males plus females) is obtained from selection in females than in males for a given selection differential. For abdominal bristle number ($r_{G_{mf}} = 0.78$) the expected response (males plus females) for a given selection differential is only 2% less for male selection than for female selection; if $r_{G_{mf}} = 0.5$, response (males plus females) from selection in males is only 6% less than from selection in females. These effects appear then to be of only minor importance unless scale effects are large and $r_{G_{mf}}$ is small.

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