

## The Nature of Quantitative Genetic Variation in *Drosophila*. II\* Average Dominance of Abdominal Bristle Polygenes

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### Abstract

A comparison of 13 abdominal bristle selection lines with their base population and with reciprocal  $F_1$ s between the selection lines and the base population was carried out. There was no significant directional contribution of maternally inherited factors to selection response.

Different estimates of average dominance ranged from 0.28 to 0.43 with a mean of 0.39. This indicates that the alleles increasing abdominal bristle number are, on average, partly recessive. Some of the possible consequences of this are discussed.

### Introduction

In diploid organisms, the dominance of alleles affects their rate of change in frequency and probability of being lost during selection (Wright 1969). Consequently, the average dominance of alleles is one of the parameters that must be specified in describing the nature of genetic variation for quantitative characters.

This series of studies is concerned with specifying the nature of genetic variation for abdominal bristle number in the Canberra population of *Drosophila melanogaster*. The objectives of this study were (1) to determine the average dominance of abdominal bristle polygenes by comparing selection lines and  $F_1$ s between selection lines and their base population, and (2) to check for maternally inherited contributions to selection response.

### Materials and Methods

The selection lines were all derived from the Canberra (Can) population (Latter 1964) and are described in detail by Frankham *et al.* (1968a, 1968b), Jones *et al.* (1968) and Hollingdale and Barker (1971). They were all selected for increased abdominal bristle number for 50 or more generations. Subsequently, they were relaxed for 40-50 generations prior to this experiment. Reciprocal crosses were carried out between the selection lines and the Can base population. The selection lines and the Can base population were also scored at the same time. For each line or cross, two bottles were set up on F media, each with five pairs of parents, and 20 females were scored per bottle.

The average dominance was computed by two methods: (1) from the regression of  $F_1$  means on parent means and (2) from the ratio of deviations from the base population of the  $F_1$  and the selection lines.

### Results

Means for the selection lines, the Can base population and the reciprocal  $F_1$ s between them are presented in Table 1 and the regression analysis of variance is presented in Table 2.

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The contribution of cytoplasmic effects and maternal components to selection response can be gauged from the differences between the reciprocal crosses, as they will result in a higher mean for the cross with the selected line mothers than the reciprocal. The means for the two crosses are 26.43 and 26.29 respectively, the difference being non-significant.

**Table 1.** Mean abdominal bristle numbers for females from the selection lines, the base population and the reciprocal crosses between them

Mean for the base population (Can) = 22.125

Line	Mean	Line <sup>A</sup> × Can F <sub>1</sub>	Can <sup>A</sup> × line F <sub>1</sub>	Line	Mean	Line <sup>A</sup> × Can F <sub>1</sub>	Can <sup>A</sup> × line F <sub>1</sub>
10(40%)b	27.975	24.675	24.350	10(20%)d	32.025	27.150	25.675
10(20%)c	30.050	26.225	25.550	20(40%)c	32.750	26.225	26.625
20(20%)c	30.075	25.775	25.275	20(20%)a	32.825	25.825	26.275
20(20%)b	30.775	25.900	25.075	0(10%)d	33.350	27.550	27.425
20(10%)b	31.075	26.325	26.525	110(20%)b	34.825	28.200	27.850
SO <sub>3</sub> <sup>+</sup>	31.550	26.075	26.450	10(20%)a	37.650	27.175	28.475
20(40%)b	31.825	26.450	27.175				

<sup>A</sup> Female parent.

In the regression analysis, the regression term is highly significant. The between-reciprocal-crosses term is highly significant and has been partitioned into a mean difference term (maternal effects) and the remainder. There is no significant average difference between reciprocal crosses, but there is a significant non-directional difference. The origin of this latter difference is not clear.

**Table 2.** Regression analysis of variance

Source	Degree of freedom	Mean square
Regression	1	697.26**
Deviation from regression	11	14.64**
Between bottles within F <sub>1</sub> s	39	6.98**
Between reciprocal F <sub>1</sub> s	13	12.02**
Maternal effects	1	5.124
Remainder	12	12.595**
Between bottles within reciprocals	26	4.45
Between individuals within bottles	988	3.87

\*\*  $P < 0.01$ .

The difference between bottles within reciprocal F<sub>1</sub>s is non-significant, but the deviation-from-regression term is significant when tested against the 'individuals' term. This significant deviation-from-regression term indicates that there are differences among lines in average dominance.

Four estimates of average dominance were obtained in this experiment. The regression of F<sub>1</sub>s (selection line female × Can male) on selection lines gives an estimate of  $0.28 \pm 0.07$  and the regression for the reciprocal cross an estimate of  $0.42 \pm 0.06$ . These do not differ significantly from each other, so the combined estimate of  $0.35 \pm 0.05$  can be used. Since the measurements of the selection line

means were subject to error, these regression coefficients may be biased downwards (Snedecor and Cochran 1967). Adjustment for this bias raises this combined estimate to 0.36, so the extent of the bias is small. Average dominance estimates from the ratio of deviations from the base population mean of the  $F_1$  and the selection lines were 0.43 and 0.42, based on the two reciprocal  $F_1$ s (pooled value of 0.426). The mean of the values from the regression and the deviation estimates is 0.39.

### Discussion

The mean difference between the reciprocal  $F_1$ s was non-significant, so the contribution of cytoplasmically inherited or other maternal components to selection response must be small. There was a significant non-directional difference among reciprocal crosses but I can offer no likely explanation for it.

The average dominance of 0.39 indicates that alleles increasing bristle number are on average slightly on the recessive side of additive. Consequently, one would expect that abdominal bristle number would increase with inbreeding in this population. This has been found by Hammond (1973).

The slight recessiveness of alleles affecting abdominal bristle number in this population contrasts with results from other populations. Clayton *et al.* (1957) concluded that the genes were additive in the Kaduna population. Kidwell and Kempthorne (1966) and Kidwell and Kidwell (1966) found no significant average change with inbreeding in the Princeton stock and concluded that the genes were additive on average. In the Orbero strain Rasmuson's (1952) results suggest that alleles were additive or slightly dominant. Consequently, it appears that *D. melanogaster* populations may differ slightly in average dominance for genes determining abdominal bristle number. There were differences in average dominance among lines in this study so there must be differences among alleles in dominance for this trait.

Sheridan *et al.* (1968) concluded that there was no dominance for this character in the Can population on the basis of statistical analyses, but they did find a sizeable additive  $\times$  additive interaction term. In the present analyses, the contributions of intralocus and interlocus effects to the average dominance cannot be determined. For example, multiplicative interactions between loci would result in deviations from additivity, even though the alleles at each locus showed additivity.

It is important to specify the consequences of partial recessiveness of alleles in comparison to those for purely additive alleles. In the first paper of this series (Frankham 1975) it was suggested that the sex-linked alleles utilized in selection lines were rare in the base population so this will be the condition considered in what follows. Some of the consequences of the partial recessiveness are:

1. The limit to selection for recessive alleles is lower than that for additive alleles at the same initial frequencies (Robertson 1960).
2. Rare recessive or partial recessive alleles may lead to irregular patterns of selection response. Such irregular patterns of selection response have been a common occurrence in selection lines from this population (Jones *et al.* 1968) but this is not the only possible explanation.
3. Rare recessive alleles lead to a longer half-life of selection response than additive alleles (Robertson 1960). In this population the half-life of selection response would be expected to be greater in selection for increased than for

decreased abdominal bristle number. No accurate estimates of half-lives of selection response are available for this population.

4. The variation among replicate populations at the selection limit for partially recessive alleles may be greater or less than for additive alleles, depending on the selection intensity, the effective population size, the initial gene frequencies and the effects of the alleles.

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