

ESTIMATES OF COVARIANCES BETWEEN FULL SIBS AND BETWEEN HALF SIBS FOR BRISTLE NUMBER AND WING LENGTH IN SAMPLES OF DROSOPHILA BRED TO VARYING LEVELS OF INBREEDING

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1. INTRODUCTION

We have the following formulae for the covariances amongst Half Sibs and Full Sibs (Kempthorne, 1957):

$$\text{Cov (HS)} = \frac{1}{4} \sigma_A^2 + 1/16 \sigma_{AA}^2 + \dots$$

and

$$\text{Cov (FS)} = \frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_B^2 + \frac{1}{4} \sigma_{AA}^2 + \dots$$

where σ_A^2 , σ_{AA}^2 and σ_B^2 represent the variances due to additive, additive \times additive, and dominant effects of genes, respectively.

It is noted that the coefficient decreases rapidly with the order of interaction. One way to increase this is to inbreed first, then:

$$\text{Cov (HS)} = \left(\frac{1+F}{4}\right) \sigma_A^2 + \left(\frac{1+F}{4}\right)^2 \sigma_{AA}^2 + \dots$$

and

$$\text{Cov (FS)} = \left(\frac{1+F}{2}\right) \sigma_A^2 + \left(\frac{1+F}{2}\right)^2 \sigma_B^2 + \left(\frac{1+F}{2}\right)^2 \sigma_{AA}^2 + \dots$$

where F is used as the inbreeding coefficient.

Obviously, prior inbreeding raises the coefficients of higher order terms, e.g. if $F=1$, then:

$$\text{Cov (HS)} = \frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{AA}^2 + \dots$$

and

$$\text{Cov (FS)} = \sigma_A^2 + \sigma_B^2 + \dots$$

Therefore, to estimate these components, one can take samples of large populations and inbreed without selection to various levels of F , and then mate at random. For each such population one can estimate Cov (HS) and Cov (FS). The experiment reported here was designed to check whether a reasonable partition of the genotypic variances is found which holds over different levels of F .

2. EXPERIMENTAL

(a) Stock

The experiments were carried out on *Drosophila melanogaster* that was kindly supplied by Dr. J. F. Kidwell, Canada Department of Agriculture. The flies were raised at 25°C following the techniques detailed in an earlier report from this laboratory (Prabhu, 1960).

(b) Breeding lines

Four random samples were taken from the original population. Each sample consisted of 150 pairs, each pair raised in a single test tube. Full sib mating was started in each sample on different days in such a manner that all the lines were ready for measurement in as short a period as possible. This ensured possible elimination of some variances between measurements. Subsequently, because of inbreeding, the number of flies per line decreased considerably.

Each of these lines was inbred to F values of 0.000, 0.250, 0.500 and 0.734, respectively. After breeding each line to a particular level of F , random mating was done by taking a male from one tube and mating it to two females each drawn from another separate tube. After mating for three days, each of the two females was transferred to a new tube containing medium. When the progeny emerged, only four females per dam were randomly collected, and the characters under study were measured on them. This plan provided data on both full and half sibs.

(c) Characters studied

Two characters were studied: (i) bristle number and (ii) wing length.

Bristle numbers on the 4th and 5th abdominal segments were counted. The counting is fairly convenient, and therefore this character has been widely used by others (Mather, 1949; Rasmuson, 1952; Taneja, 1956, 1957; and others). The sum of the counts of bristles on the 4th and 5th abdominal segments was used in the entire experiment since the repeatability, as discussed later, of the sum for the two segments was higher than that for each individual segment.

Wing length was measured in mm. This measurement was taken along the length of the 4th longitudinal vein extending from the second basal cell to its termination at the tip of the wing. The procedure adopted was essentially the same as used by Robertson and Reeve (1952b).

(d) Statistical analysis

(i) Algebraic model:—The following model was used for the estimation of components of variances.

Suppose there are m sires, the i th sire mated to n_i dams; and a random sample of p_{ij} offspring is measured from each sire-dam mating. The model is:

$$\begin{aligned}
 Y_{ijk} &= u + s_i + d_{ij} + e_{ijk} \\
 i &= 1, 2, \dots, m \\
 j &= 1, 2, \dots, n_i \\
 k &= 1, 2, \dots, p_{ij}
 \end{aligned}$$

Y_{ijk} is the observation (bristle number or wing length) on the k th offspring of the j th dam mated to i th sire; s_i , d_{ij} and e_{ijk} are random variables normally and independently distributed with means zero and variances σ_s^2 (between sires), σ_d^2 (between dams) and σ_e^2 (between full sibs), respectively.

The mean squares and their expectations are given in Table 1.

Table 1. *Mean Squares and Expectations*

Source of variation	d.f.	M.S.	E (M.S.)
Between sires	$(m-1)$	V_1	$\sigma_e^2 + k_2\sigma_d^2 + k_3\sigma_s^2$
Between dams within sires	$\sum_i (n_i-1)$	V_2	$\sigma_e^2 + k_1\sigma_d^2$
Between full sibs	$\sum_{ij} (p_{ij}-1)$	V_3	σ_e^2

$$V_1 = \frac{1}{m-1} \left[\sum_i \frac{Y^2_{i..}}{p_{i.}} - \frac{Y^2_{...}}{p_{..}} \right]$$

$$V_2 = \frac{1}{\sum_i (n_i-1)} \left[\sum_{ij} \frac{Y^2_{ij.}}{p_{ij}} - \sum_i \frac{Y^2_{i..}}{p_{i.}} \right]$$

$$V_3 = \frac{1}{\sum_{ij} (p_{ij}-1)} \left[\sum_{ijk} Y^2_{ijk} - \sum_{ij} \frac{Y^2_{ij.}}{p_{ij}} \right]$$

Therefore the estimates of σ_s^2 , and σ_d^2 are derived by substituting the values of k_1 , k_2 , and k_3 which were estimated as under:

$$k_1 = \frac{1}{\sum_i (n_i-1)} \left[p_{..} - \sum_{ij} \frac{p^2_{ij}}{p_{i.}} \right]$$

$$k_2 = \frac{1}{(m-1)} \left[\sum_{ij} \frac{p^2_{ij}}{p_{i.}} - \sum_{ij} \frac{p^2_{ij}}{p_{..}} \right]$$

$$k_3 = \frac{1}{(m-1)} \left[p_{..} - \sum_i \frac{p^2_{i.}}{p_{..}} \right]$$

(ii) *Covariances*:— The covariances between full sibs and between half sibs were

determined from the components of variance as suggested by Falconer (1960), and these are as below:

$$\text{Cov (HS)} = \sigma_r^2$$

$$\text{Cov (FS)} = \sigma_r^2 + \sigma_d^2$$

(iii) *Repeatabilities*:—In order to determine the extent to which an operator is capable of repeating his own observations, a product moment correlation between his two repeated measurements on a sample of 25 flies was estimated. For this, the character was first measured on each of the 25 flies, and the measurement was again repeated without any reference to the first measurement.

3. RESULTS

(a) Mean values

Results presented in Table 2 indicate that the mean chaeta number did not decrease with increase in the level of inbreeding. Wing length, on the other hand, showed slight reduction in size.

Table 2. *Mean values and standard deviations for bristle number and wing length in different samples of Drosophila melanogaster bred to varying levels of inbreeding*

Inbreeding coefficient (F)	0.000	0.250	0.500	0.734
<i>Bristle number:</i>				
Mean	41.163	41.351	42.210	41.265
S.D.	5.406	4.711	5.054	5.041
% C.V.	13.13	11.39	11.97	12.21
<i>Wing length:</i>				
Mean	1.748	1.744	1.737	1.730
S.D.	0.079	0.077	0.068	0.143
% C.V.	4.51	4.41	3.32	8.25

Standard deviations calculated on the basis of total variation in each line.

(b) Repeatabilities

The repeatability estimates for each of the two characters are given below:

Characters	<i>r</i>
Bristles on 4th segment	0.782
Bristles on 5th segment	0.764
Bristles on 4th and 5th combined	0.810
Wing length	0.827

Repeatability estimates are fairly high for both the characters. Since the repeatability of bristles on the 4th and 5th segments together is higher than for each individual segment, the sum of bristles on the 4th and 5th segments was used as the metric character.

(c) *Analysis of variance*

Results of the analysis of variance presented in Table 3 indicate that the variances between sires and between dams within sires for bristle number were not significant in any of the four lines. In the case of wing length, the variances between sires were significant in two lines only. The differences between dams within sires were significant for only one line.

The mean square between dams within sires for wing length for $F = 0.000$ was smaller than the mean square between full sibs. This is due to sampling errors.

The components of variance derived from Table 3 are presented in Table 4.

Table 3. *Results of analysis of variance*

Inbreeding coefficient (F)	0.000		0.250		0.500		0.734	
	d.f. ⁽³⁾	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
<i>Bristle number:</i>								
Between sires	.. 44	12.141	22	10.520	19	13.910	7	13.871
Between dams within sires	45	9.841	23	6.815	20	6.640	8	6.156
Between full sibs	.. 270	7.253	138	5.656	117	5.000	48	5.391
<i>Wing length:</i>								
Between sires	.. 44	0.00358*	20	0.00292	19	0.00264**	9	0.01369
Between dams within sires	45	0.00132	21	0.00176	20	0.00118	8	0.00518*
Between full sibs	.. 225	0.00142	107	0.00126	92	0.00082	52	0.00163

**significant at 1% level of probability

*significant at 5% level of probability

(d) *Covariances between full sibs and between half sibs*

The results shown in Table 5 and Figs. 1 and 2 indicate that the estimates of covariances for bristle number increased linearly with increase in the level of inbreeding.

In the case of wing length, on the other hand, there was on the average a slight increase up to the level of $F=0.500$, but subsequently there was a sharp rise in the estimates of covariances when the F value of 0.734 was reached.

Table 4. *Components of variances derived from Table 3*

Inbreeding coefficient (F)		0.000	0.250	0.500	0.734				
<i>Bristle number:</i>									
σ_s^2	0.290	0.464	0.922	1.092
σ_d^2	0.655	0.289	0.422	0.194
σ_c^2	7.253	5.656	5.000	5.391
σ_t^2	8.198	6.409	6.344	6.677
<i>Wing length:</i>									
σ_s^2	0.00031	0.00033	0.00022	0.00122
σ_d^2	0.00000	0.00016	0.00011	0.00091
σ_c^2	0.00142	0.00126	0.00082	0.00163
σ_t^2	0.00173	0.00175	0.00115	0.00376

$\sigma_s^2, \sigma_d^2, \sigma_c^2, \sigma_t^2$, denote components due to sire, dam, full sib, and total respectively.

Table 5. *Estimates of covariances between full sibs (Cov (FS)) and between half sibs (Cov (HS)) for bristle number and wing length in different samples of *Drosophila melanogaster* bred to varying levels of inbreeding*

Inbreeding coefficient (F)			0.000	0.250	0.500	0.734	
<i>Bristle number:</i>							
Cov (FS)	0.945	0.753	1.344	1.286
Cov (HS)	0.290	0.464	0.922	1.092
<i>Wing length:</i>							
Cov (FS)	0.00031	0.00049	0.00033	0.00213
Cov (HS)	0.00000	0.00033	0.00022	0.00122

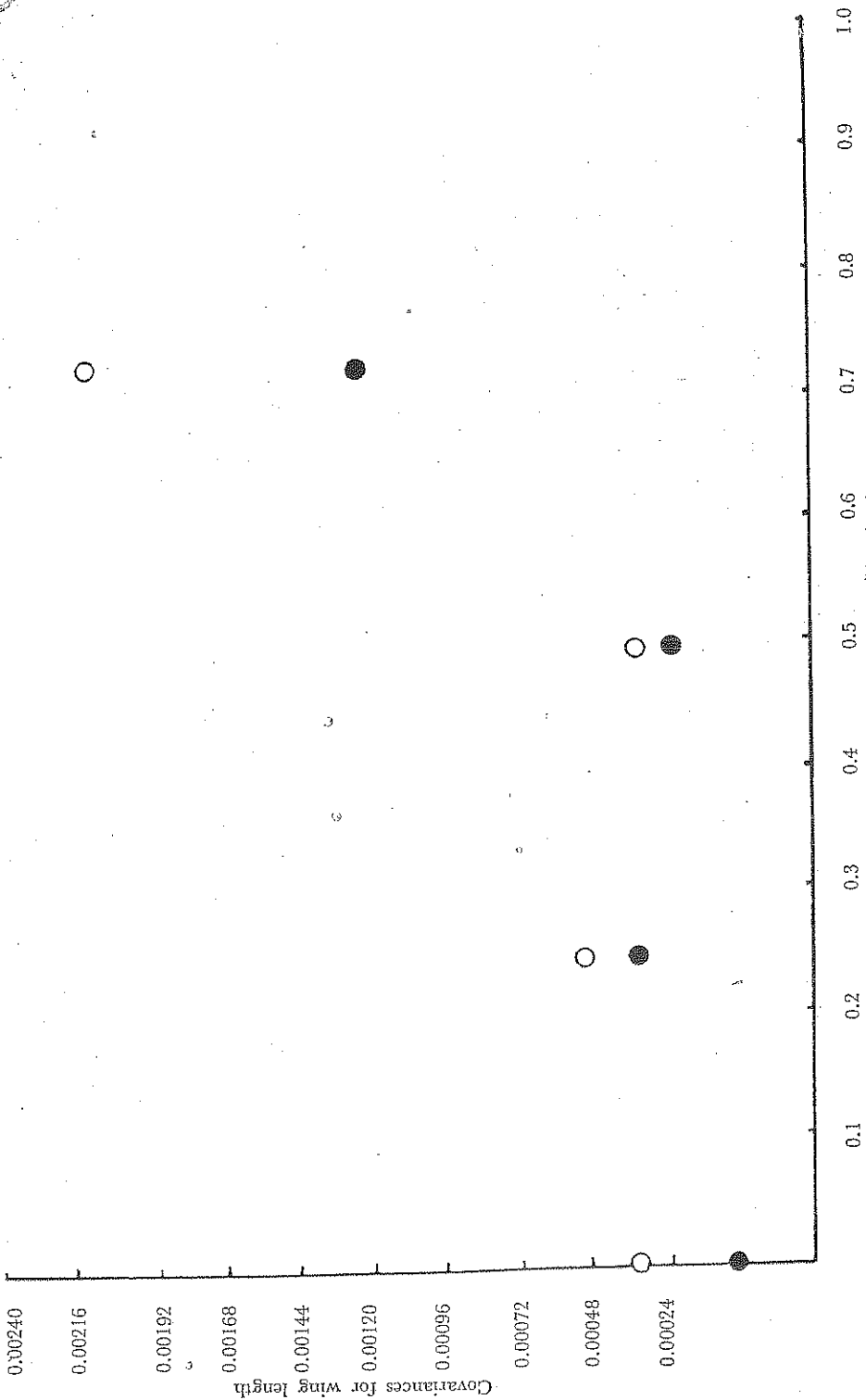


Figure 1. Relationship between covariances for full sibs (O) and for half sibs (●) and inbreeding coefficient for wing length in *Drosophila melanogaster*.

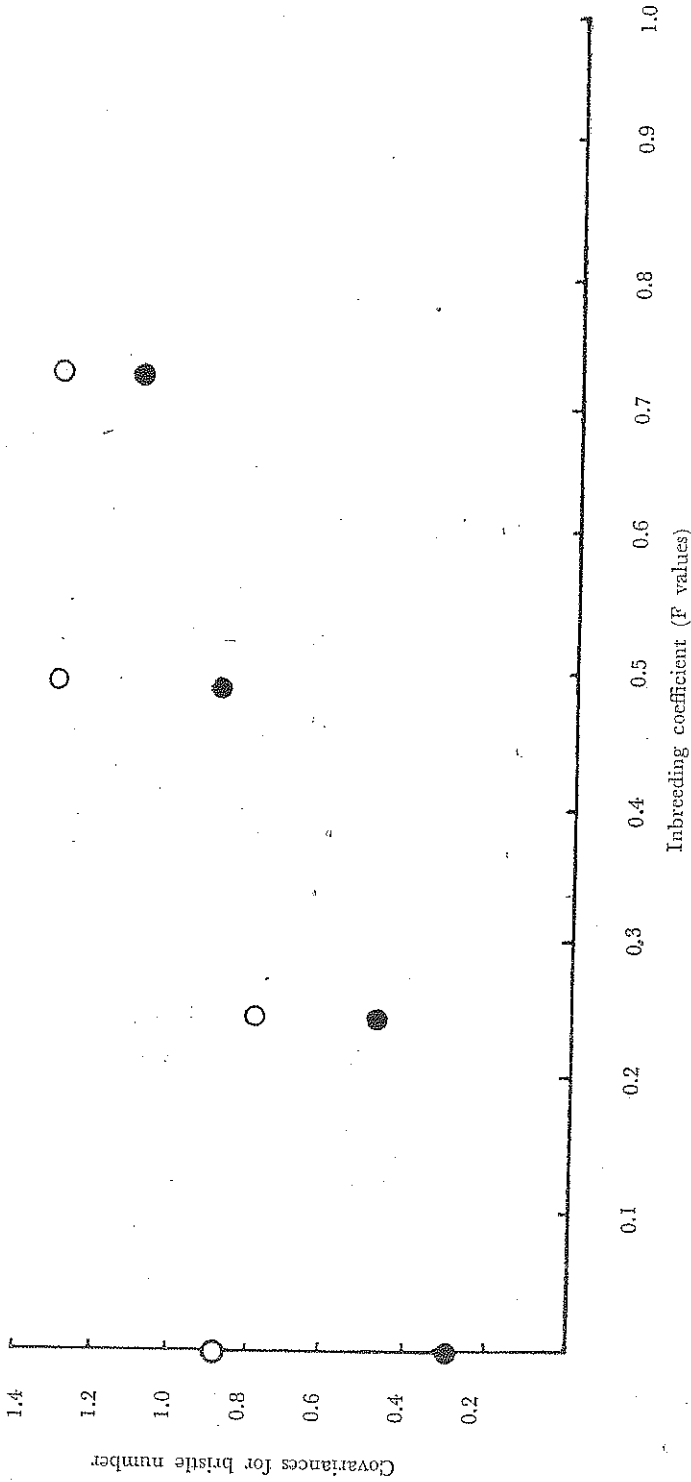


Figure 2. Relationship between covariances for full sibs (O) and half sibs (●) and inbreeding in *Drosophila melanogaster*.

4. DISCUSSION

So far as the authors are aware, this is the first report to check the theoretical expectations of covariances between full sibs and between half sibs at different levels of inbreeding for bristle number and wing length in *Drosophila*. The results have shown that, on the average, the full sib covariances for bristle number are twice as much as those of half sibs, and these estimates have risen linearly in relation to the increase in the level of inbreeding. Therefore, they show reasonable agreement between the theoretical expectations and the actual estimates.

In the case of wing length there is, on the average, some increase in the covariances when the F value of 0.500 is reached, although this increase is very small. At $F=0.734$, the covariance again increases considerably, therefore, the data on the covariances between full sibs and between half sibs present a curvilinear increase with concavity towards the axis representing F values. These differences in the pattern of covariances amongst relatives for the two characters may be due to their relative importance for fitness. Bristle number contributes little towards fitness whereas wing length is vital for existence. It is possible that inbreeding tending to cause reduction in the size of the wing resulted in the elimination of such genotypes which were not able to compete for the food. This elimination of genotypes did not permit the relationship amongst sibs to rise with increase in the level of inbreeding.

In *Drosophila*, the X chromosome has an important influence on quantitative characters (Wigan, 1948). The calculations for F values apply to fully diploid organisms or those such as most mammals where autosomal genes may be neglected. In *Drosophila*, $\sigma\beta$ does not exist for the sex linked genes of males. And F' , which measures homozygosity at sex linked loci in females is not usually the same as F . Therefore for our system of mating the F' values were calculated and they were 0.000, 0.125, 0.180, and 0.197 for the corresponding values 0.000, 0.025, 0.500 and 0.734, respectively of F . The pattern of relationship between the Cov (HS) and Cov (FS) with F' remains the same as with F .

Our results suggest that chaeta number does not decrease with increase in inbreeding. This is not surprising since the characters that contribute little towards fitness such as bristle number in *Drosophila* show little change in mean values with increase in inbreeding. Only the vital components of fitness connected with reproductive capacity and other physiological functions are affected with increase in the level of inbreeding. This is fully supported by our data since out of 150 pairs that were set up in each line, only 135, 69, 60 and 24 were left alive for the F values of 0.000, 0.250, 0.500 and 0.734, respectively. This shows a linear decline in survival rate with increase in inbreeding.

It is well known that inbreeding causes increase in the environmental variance, and the causes for this have been discussed by several workers (Robertson and Reeve, 1952a; Mather, 1953; Haldane, 1954; and others). However, when inbred lines are crossed, the variance in the crosses is smaller than the variance in the inbred lines (Robertson and Reeve, 1952a; Rasmuson 1952). Robertson and Reeve (1952a) found that the variance of wing length in the crosses between inbred lines was reduced to nearly half

of the parental average. Rasmuson (1952) also observed that the F_1 s between inbred lines had a lower variance than the inbred lines themselves or the original strains. In the present study inbred individuals from different cultures with the same level of inbreeding were crossed and perhaps this resulted in reducing the environmental variance represented by $(\sigma_e^2 + \sigma_d^2 - 3\sigma_i^2)$.

Theoretically, σ_d^2 should be larger than σ_i^2 , if non-additive genetic variance is present. In our data only in one line for bristle number ($F=0.000$) was σ_d^2 larger than σ_i^2 . Therefore, on the average, the non-additive genetic variance in these data did not exist. Assuming that the estimate of $\sigma_d^2 - \sigma_i^2$ in bristle number for the line with $F=0$ is real and is not attributable to sampling errors, the partitioning of the phenotypic variance can be done. This has been estimated as under:

Phenotypic variance	100
Additive genetic variance	14
Non-additive genetic variance	7
Environmental, general	10
Environmental, special	69

Our estimate on non-additive genetic variance is well in agreement with that reported by others, although the values for additive genetic variance are low (Clayton, Morris and Robertson, 1957; Reeve and Robertson, 1954). These differences may be due to sampling errors apart from the differences in stock and environmental conditions.

5. SUMMARY

Covariances between full sibs and between half sibs were estimated for bristle number and wing length in different samples of *Drosophila melanogaster* bred to varying levels of inbreeding. The estimates for bristle number increased linearly with increase in F values, but for wing length the trend appeared curvilinear with concavity towards the axis representing F values.

Mean chaeta number was not affected by the level of inbreeding, although there was an apparent trend in the reduction of wing length. Inbreeding depression measured by the number of flies which survived in each line was very apparent.

Non-additive genetic variance was found to be unimportant in these data.

The phenotypic variance, on the average, tended to decrease slightly with increase in inbreeding.

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