

# FURTHER 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

BY G. C. TANEJA\*, SWASTIKA RAWAT† AND SATISH KUMAR

*Animal Genetics Division,  
Indian Veterinary Research Institute, Izatnagar (UP), India*

## I. INTRODUCTION

The theoretical values for the correlations between relatives have been worked out by several workers (see Kempthorne, 1957 for references). Kempthorne (1957) reported theoretical expectations of covariances amongst relatives in different populations arising by inbreeding to various degrees. Taneja and Negi (1963) applied these theoretical expectations of covariances to their data on *Drosophila* to find out to what extent these formulae were correct biologically. These authors reported that the estimates of covariances between full sibs and between half sibs for bristle number showed reasonable agreement with the theoretical expectations, but similar estimates for wing length showed curvilinearity with concavity towards the axis representing the  $F$  values. It was, therefore, concluded that in the case of wing length the elimination of some genotypes did not permit the relationship amongst sibs to rise with increase in the level of inbreeding. Since these workers used only 4 populations, each with a few inbred lines varying from 135 to 24 only, the results could not be generalised, and further scope for work in the subject became obvious. Therefore, the experiment reported here was started with 8 populations, each with a large number of inbred lines varying from 375 to 108 to check the theoretical expectations of covariances between full sibs and between half sibs for bristle number and wing length in *Drosophila melanogaster*.

## II. EXPERIMENTAL

### (a) Stock

A wild stock of *Drosophila melanogaster* trapped from Izatnagar area was used in these experiments. Ten pairs of flies were kept in each of 9 bottles and allowed to lay eggs. When the progeny emerged, 10 virgin pairs from each bottle were collected and mixed and again distributed into 9 bottles for further propagation of flies. The flies which then emerged constituted the foundation stock for these experiments.

The flies were raised in a constant temperature cabinet placed in an air-conditioned laboratory in which the temperature varied from 22 to 28°C. The temperature in the

\*Present address: Division of Special Animal Studies, Central Arid Zone Research Institute, Jodhpur (Rajasthan), India.

†Formerly Swastika Negi.

constant temperature cabinet was  $25 \pm 1^\circ\text{C}$ . The bottles or the test tubes in which the flies were raised contained Burdick medium (Burdick, 1954). On the average, the food and temperature conditions of the experimental stock were uniform throughout the period of work.

(b) *Inbred Populations*

Eight random samples were taken from the foundation stock. Each sample consisted of 375 pairs, each pair raised in a single test tube. Full sib mating was done in each tube. The populations which were to be bred to a high level of inbreeding were started first and those required for a low level were started later. In this way, the breeding programme was arranged in such a manner that all populations bred to varying levels of inbreeding, were ready for measurement in as short a period as possible. This ensured possible elimination of some variances between measurements.

Each of these 8 populations were inbred to  $F$  values of 0.000, 0.250, 0.375, 0.500, 0.672, 0.734, 0.785 and 0.908 respectively. After breeding each population to a particular level of  $F$ , random mating was done by taking a male from one tube and mating it to two females, drawn from different, separate tubes. After mating for three days, each female 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 sibs 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 sum of the counts of bristles on the 4th and 5th segments was used in the entire experiment since the repeatability of the sum for the two segments was higher than that for each segment (Taneja and Negi, 1963).

The 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 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:

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

$Y_{ijk}$  is the observation (bristle number or wing length) on the  $k$ th offspring of the  $i$ th dam mated to  $i$ th sire;  $s_{ij}$ ,  $d_{ij}$  and  $e_{ijk}$  are taken to be random variables normally and independently distributed with means zero and variances  $\sigma_s^2$  (between sires),  $\sigma_d^2$  (between dams) and  $\sigma_e^2$  (between full sibs) respectively.

The methods of calculation of mean squares and their expectations used for the estimation of components of variances were the same as described earlier (Taneja and Negi, 1963).

(ii) *Covariances*: Covariances between full sibs and between half sibs were determined from the components of variances as suggested by Falconer (1960), and these are as below:

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

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

(iii) *Heritabilities*: Estimates of heritabilities ( $h^2$ ) were made from half sib ( $G_{r(HS)}$ ) and full sib ( $G_{r(FS)}$ ) correlations (Falconer, 1960).

$$4 G_{r(HS)} = h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}; \quad 2G_{r(FS)} = h^2 = \frac{2(\sigma_s^2 + \sigma_d^2)}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}.$$

### III. RESULTS

#### (a) Mean values

Results presented in Table 1 indicate that the mean chaeta number increased with increase in the level of inbreeding. The increase, was, however, not statistically significant ( $t_6=2.044$ ;  $t_{.05}=2.477$ ). The wing length on the other hand showed a slight decrease with the level of inbreeding. The decrease was, however, not significant ( $t_6=0.273$ ,  $t_{.05}=2.447$ ).

Table 1. 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	0.375	0.500	0.672	0.734	0.785	0.908
Bristle number:								
Mean	46.301	47.200	47.420	46.417	47.018	47.258	47.552	47.604
S.D.	3.843	3.935	3.765	4.062	4.092	3.681	3.702	3.686
C.V. %	8.300	8.337	7.940	8.751	8.703	7.789	7.785	7.743
Wing length:								
Mean	1.805	1.929	1.863	1.850	1.801	1.805	1.867	1.853
S.D.	0.050	0.042	0.044	0.048	0.038	0.038	0.042	0.039
C.V. %	2.770	2.177	2.362	2.595	2.110	2.105	2.249	2.105

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

In the case of bristle numbers, the variance increased up to an  $F$  value of 0.500 and tended to decline after that. The variance for wing length, declined with increase in  $F$  value from 0 to 0.908.

(b) *Analysis of variance*

Results of the analysis of variance presented in Table 2 are summarised below:

(i) *Bristle number:*

(1) There were highly significant differences between dams within sires in all the populations bred to varying levels of inbreeding.

(2) The variance between sires and between dams increased with increase in  $F$  value up to 0.672 and 0.500 respectively and it tended to decline afterwards to reach the original level at  $F=0$ .

(3) The variance between full sibs rose slightly up to  $F=0.25$  and tended to decline afterwards with increase in inbreeding.

(ii) *Wing length:*

(1) The differences between sires were significant in all populations except in those with  $F$  values of 0.000, 0.500, and 0.908. The differences between dams within sires were, however, significant in all populations.

(2) The variance between sires did not show any particular trend in relation to the level of inbreeding.

(3) The variance between dams gradually decreased with increase in inbreeding and the variance at  $F=0.908$  was much lower than the value at  $F=0$ .

(4) The variance between full sibs decreased after  $F=0.250$ , and it remained steady after that except for some rise at  $F=0.500$ .

The components of variances derived from Table 2 are presented in Table 3.

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

The results on covariances presented in Table 4 indicate the following points:

(i) *Bristle number:*

The covariances between full sibs and between half sibs for bristle number showed a rising trend with increase in the level of inbreeding. Both linear and curvilinear regressions of the estimates of covariances between half sibs ( $\mathcal{Y}$ ) on  $F$  values ( $x$ ) were calculated with the following equations:

$$\mathcal{Y} = 2.147 + 1.166x$$

$$\mathcal{Y} = 2.272 + 0.237x + 1.012x^2.$$

Regression coefficients were not significant. In linear regression analysis,  $x$  accounted only for 12.7% of the total variation in  $\mathcal{Y}$ . In the curvilinear regression analysis the second degree term accounted for 11.8% of total variation in  $\mathcal{Y}$ . Thus, statistically, there was no significant rise in estimates of covariances either in a linear or in a quadratic manner.

Table 2. Results of analysis of variance

	0.000		0.250		0.375		0.500		0.672		0.734		0.785		0.908	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Bristic number:																
Between sites	116	37.750**	108	35.916**	85	39.320**	86	43.784*	59	53.016**	57	53.394**	53	46.594**	35	39.995**
Between dams with- in sites	110	18.210**	99	21.738**	68	18.939**	71	32.083**	51	20.291**	54	20.063**	48	18.233**	33	17.905**
Between full sibs	675	10.410	620	10.505	450	8.569	478	9.283	323	9.564	326	8.653	295	7.063	207	8.441
Wing length:																
Between sites	116	0.0033895	108	0.004239**	85	0.003930**	86	0.004406	59	0.003170*	57	0.004234**	53	0.005400**	35	0.008116
Between dams with- in sites	107	0.008756**	99	0.003903**	68	0.005402**	69	0.005591**	51	0.002297**	54	0.002070**	48	0.003133**	33	0.002750**
Between full sibs	550	0.002032	405	0.000843	416	0.000906	404	0.001090	300	0.000941	302	0.000812	274	0.000865	183	0.000978

\*\*Significant at 1% level of probability  
\*Significant at 5% level of probability

Table 3. Components of variances derived from Table 2.

Inbreeding Coefficient (F)	0.000	0.250	0.375	0.500	0.672	0.734	0.785	0.908
Bristle number:								
$\sigma_a^2$	2.244	2.080	2.935	1.601	4.525	1.875	3.803	2.886
$\sigma_d^2$	1.693	2.985	2.726	5.700	2.747	3.178	2.927	2.366
$\sigma_s^2$	10.548	10.505	8.569	9.283	9.564	8.653	7.063	8.441
$\sigma_t^2$	14.485	15.520	14.230	16.584	16.836	13.706	13.793	13.693
Wing length:								
$\sigma_a^2$	0.000006	0.000323	0.000374	0.000117	0.000121	0.000291	0.000432	0.000051
$\sigma_d^2$	0.000514	0.000899	0.000706	0.000540	0.000374	0.000373	0.000636	0.000480
$\sigma_s^2$	0.002032	0.000843	0.000906	0.001690	0.000941	0.000812	0.000865	0.000978
$\sigma_t^2$	0.002552	0.002075	0.001986	0.002347	0.001436	0.001376	0.001933	0.001509

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

Table 4. 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	0.375	0.500	0.672	0.734	0.785	0.908
Bristle number:								
Cov (FS)	3.937	5.015	5.661	7.301	7.272	5.053	6.730	5.252
Cov (HS)	2.244	2.030	2.935	1.601	4.525	1.875	3.803	2.886
Wing length:								
Cov (FS)	0.000520	0.001222	0.001080	0.000657	0.000495	0.000664	0.001068	0.000531
Cov (HS)	0.000006	0.000323	0.000374	0.000117	0.000121	0.000291	0.000432	0.000051

Similarly, both linear and curvilinear regressions were fitted to full sib data with the following equations:

$$Y = 4.753 + 1.941x$$

$$Y = 3.658 + 10.021x + 8.796x^2.$$

Neither the linear nor the curvilinear regression coefficients were significant. In the linear equation, the  $x$  accounted for 24% of the variation in  $Y$ , which was not significant. In the curvilinear regression, the multiple correlation coefficient,  $R^2=0.53$  was not significant. Although a high value of  $R$  was obtained, due to the relatively small number of observations, it did not approach significance.

(ii) *Wing length:*

The covariances between full sibs and between half sibs increased up to an  $F$  value of 0.375, and decreased again at  $F$  values of 0.500 and 0.672 followed with a rise at  $F=0.785$  and fall at  $F=0.908$ . Therefore, the estimates fluctuated with the rise in the level of inbreeding and did not present any specific trend.

(d) *Estimates of heritabilities*

The estimates of heritabilities for wing length and bristle number in different populations bred to varying levels of inbreeding are presented in Table 5. These estimates, unlike those of covariances (Table 4), take into account the variance due to the environment, but still show the same trend as those for covariances.

Table 5. *Estimates of heritabilities*

Inbreeding Coefficient (F)	0.000	0.250	0.375	0.500	0.672	0.734	0.785	0.908
Bristle number:								
$\frac{2(\sigma_s^2 + \sigma_d^2)}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$	0.544	0.646	0.796	0.880	0.864	0.737	0.976	0.767
$\frac{4\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$	0.620	0.523	0.825	0.386	1.075	0.547	1.103	0.843
Wing length:								
$\frac{2(\sigma_s^2 + \sigma_d^2)}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$	0.408	1.178	1.087	0.559	0.690	0.965	1.105	0.704
$\frac{4\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_e^2}$	0.010	0.623	0.752	0.199	0.336	0.845	0.894	1.282

IV. DISCUSSION

Taneja and Negi (1963) reported that, on the average, the full sib covariances for bristle number were twice as much as those of half sibs, and the estimates increased

linearly in relation to the increase in the level of inbreeding. The results of the present study confirm our previous findings. However, the data in this study were twice as large as those reported earlier, and therefore provided more precise estimates. The results have shown that statistically there is no significant rise in the value of covariances between full sibs or between half sibs with an increase in the level of inbreeding.

So far as the trend in the estimates of covariances in relation to levels of inbreeding is concerned, there is reasonable agreement between the estimated and the theoretical values. If we consider the estimates of covariances in a random bred population ( $F=0$ ) as the true estimates, the expected values of these estimates for each inbred population can be worked out, using the formulae already described by Taneja and Negi (1963). However, since the estimated covariances between half sibs in a random bred population were lower than those at  $F=0.250$ , it appears that these differences are due to sampling errors. Therefore, the estimated values for covariances for the population with  $F=0.250$  may be used instead of those estimated for random bred population. The estimated and expected values of covariances between full sibs and between half sibs for bristle number are as under.

Inbreeding coefficient	Cov (HS)		Cov (FS)	
	Expected	Estimated	Expected	Estimated
0.000	2.030	2.147	3.937	4.753
0.250	2.736	2.449	4.921	5.238
0.375	2.793	2.456	5.331	5.481
0.500	3.045	2.484	5.906	5.724
0.672	3.394	2.522	6.583	6.059
0.734	3.516	2.536	6.827	6.178
0.785	3.622	2.547	7.024	6.277
0.908	3.873	2.575	7.520	6.515

The covariance estimates for full sibs are more reliable than those for half sibs, because the former are calculated by adding the sire and dam components ( $\sigma_s^2 + \sigma_d^2$ ) and this should eliminate some of the sampling errors. In population with inbreeding coefficients below 0.500, the estimated values for covariances between full sibs tend to be higher than the expected values and in populations with inbreeding coefficients higher than 0.500, the estimated values are below the expected ones. It would, therefore, appear that "too little" and "too much" inbreeding are partially compensated for.

The estimates of covariances on wing length do not present any specific trend. After an initial rise at  $F=0.250$  it tended to decline gradually till  $F=0.785$  was reached when it rose again followed with a fall at  $F=0.908$ . The rise in the relationship



amongst individuals at  $F=0.250$  and  $F=0.785$  may be due partly to common environmental variation which contributes chiefly to the resemblance between sibs. In an earlier study (Taneja and Negi, 1963) it was observed that the covariances amongst sibs showed a curvilinear increase with concavity towards the axis representing  $F$  values. The present study did not confirm our earlier findings.

The results of this study as well as the earlier work suggest clearly that the covariances for wing length, unlike those for bristle number, do not follow the expected theoretical trend. These differences in the pattern of covariances among relatives for the two characters may be due to their relative importance for fitness. Bristle number contributes little towards fitness whereas wing length does.

In the case of bristle number, only in three populations ( $F=0.250$ ,  $0.500$  and  $0.734$ ) is  $\sigma^2_d$ , the dam component, greater than  $\sigma^2_s$ , the sire component, thus indicating the non-additive effects of genes. Data on wing length, however, show that  $\sigma^2_d$  is larger than  $\sigma^2_s$  in all the eight populations. Our data therefore allow the estimation of dominance for the characters in question.

If there is random mating in a population and there is no linkage,

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

and

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

If the parents are individuals arising by inbreeding to degree  $F$  in such a population, then (Cockerham, 1954; Kempthorne, 1957)

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

and

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

If the parents are completely inbred

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

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

$$\therefore \sigma_B^2 = \text{Cov (FS)} - 2 \text{Cov (HS)} \text{ (neglecting interactions),}$$

$$\sigma_g^2, \text{ the additive genetic variance} = \text{Cov (HS),}$$

and the average degree of dominance "a" is estimated as under:

$$"a" = \frac{\sigma_B^2}{\sigma_g^2} = \frac{\text{Cov (FS)} - 2 \text{Cov (HS)}}{\text{Cov (HS)}} \quad (1)$$

If the lines are inbred to varying levels of inbreeding  $0.000$ ,  $0.250$ ,  $0.375$ ,  $0.500$ ,  $0.672$ ,  $0.734$ ,  $0.785$  and  $0.908$ , as in this study, the term in (1) may be multiplied by  $1.00$ ,  $0.80$ ,  $0.73$ ,  $0.67$ ,  $0.60$ ,  $0.58$ ,  $0.56$ ,  $0.52$  respectively for the estimation of "a". It will be seen that for  $F=0$ , the equation in (1) turns out to be:

$$"a" = \frac{2\sigma_B^2}{\sigma_g^2}$$

The estimates of average degrees of dominance, "a", for various inbred populations for wing length are given below.

Inbreeding coefficient	Degree of dominance
0.000	11.660
0.250	1.629
0.375	1.138
0.500	2.301
0.672	1.466
0.734	0.570
0.785	1.816
0.908	2.957

The high value of 11.660 in  $F=0$  is apparently due to sampling errors. Comstock and Robinson (1948) stated that if "a" is greater than zero, a degree of dominance in the action of genes conditioning the character in question is indicated. If it is greater than one, overdominance is indicated. The tests of significance applied to our data suggest that the estimates are significantly greater than zero. Except for one estimate of "a" all other values are greater than one and, therefore, it is probable that there is considerable variation due to over dominance of genes in this character. This confirms the earlier findings of Reeve and Robertson (1953). Further, Lerner (1954) has also concluded that over-dominance with respect to fitness and characters closely connected with it is a widespread and very important phenomenon. A contrary view is, however, expressed by Mathur (1955) that much of what appears to be over-dominance with respect to certain characters in plants can be attributed to epistatic interaction. These two conflicting opinions appear to show that the problem of over-dominance still remains an open question.

In this study, inbreeding has not affected the mean chaeta number or the wing length. Pantawy and Reeve (1956) and Taneja and Negi (1963) have, however, shown that inbreeding causes reduction in the size of wing length. If the genes that increase the value of the character are dominant over their alleles that reduce the value, then inbreeding will result in a reduction of the population mean. We are, therefore, unable to explain the failure of inbreeding to cause reduction in wing length, particularly when some of the variation has been found to be due to dominant effects of genes.

It is well known that inbreeding causes an increase in environmental variance, and the causes for this have been discussed by several workers (Robertson and Reeve, 1952a; Mathur, 1953; Haldane, 1954; and others). Our results suggest that, to a certain extent the total variance increases with increase in the level of inbreeding and beyond this it tends to decrease. The total variance in each of the two characters increased up to  $F=0.500$  and after that it tended to decline. Apparently, beyond a level, the

inbreeding steadily weeded out such individuals as were tending to adopt themselves to extreme environment and only those which were capable of living in a relatively more uniform environment survived.

#### V. SUMMARY

Eight populations of *Drosophila melanogaster* were raised to varying levels of inbreeding:  $F=0.000, 0.250, 0.375, 0.500, 0.672, 0.734, 0.785$  and  $0.908$ . Estimates of covariances between full sibs and between half sibs for bristle number and wing length were made in each of these populations. The estimates for bristle number showed a linear rise with increase in  $F$  values. Statistically, the rise was not significant. The estimate for wing length did not show any specific trend in relation to the level of inbreeding. The results are discussed in the light of theoretical expectations.

Neither mean chaeta number nor mean wing length was affected by inbreeding.

Variation due to dominant effects of genes for wing length was found in all the populations. Three populations also showed non-additive genetic variation for bristle number.

The phenotypic variance tended to increase with increase in the level of inbreeding up to  $F=0.500$  and beyond this, it tended to decline.

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