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The nature of the purebred–crossbred genetic covariance*

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SUMMARY

Epistatic models are examined for conditions which result in a negative covariance between a sire's purebred and test-cross progenies. It is found that heterozygote superiority is not a necessary condition for its occurrence. The frequencies of the same allele in the selected population and in the tester should be divergent. The implications of using the covariance in prediction are discussed. The important result to note is that selection in the crossbred may not be optimum even with a negative covariance.

1. INTRODUCTION

A major problem in applied breeding is the plateau of selection response when genetic variance persists. A theoretically simple cause is the superiority of heterozygotes for the selected trait. Since various cross-line selection schemes have been designed to exploit such gene action, the breeder needs some method of ascertaining its existence in his selection lines. Bowman (1960) has presented a technique for detecting overdominance. The procedure involves the covariance between a sire's purebred and crossbred progenies; for the simplest model of two alleles at a single locus, a negative covariance can occur only if the locus exhibits overdominance.

Several authors have considered this technique when investigating the nature of gene action. Bowman (1960) reported negative correlations for lines of mice selected for increased litter size and for lines of *Drosophila* selected for decreased number of abdominal chaetae. However, these were not significant relative to their standard errors. Wilson *et al.* (1962) found negative correlations (in the neighbourhood of $-0{\cdot}2$) for litter size and for litter weight in swine, but these were associated with such large standard errors that they were unwilling to conclude that overdominance was involved. In two closed populations of poultry previously selected for many generations on purebred performance and currently under reciprocal recurrent selection, Krause, Yamada & Bell (1965) found positive correlations in both populations for sexual maturity (a highly heritable trait) and in one population for percentage egg production (a poorly heritable trait). A

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negative correlation was found for the latter trait in the second population; however, all of these correlations were small and non-significant. Biswas & Craig (1969) found highly positive correlations for egg production and relegated no importance to overdominance in two newly synthesized poultry populations under reciprocal recurrent selection.

The purpose of this paper is to examine epistatic models to determine whether the covariance technique is valid beyond the one-locus model.

2. EPISTATIC MODELS

The general model for determining the purebred–crossbred covariance is presented in detail by Griffing (1962). For two loci, the covariance is a function of additive effects and additive × additive effects. Here we will consider two infinite populations, one designated 'Tester' and the other 'Selected', with two alleles at each of two unlinked loci. Let A, a be the two alleles at one locus and B, b the two alleles at the other locus.

To determine the relation of epistasis to the occurrence of a negative covariance, various kinds of models were examined. Two well-known models of epistasis, the complementary and duplicate models, yielded only positive covariances for all combinations of gene frequencies. These models are quite *regular* in the sense that a gene substitution at either locus produces no change in genotypic value or produces a change in only one direction regardless of the remaining gene content. For an *irregular* epistatic model there would exist a locus at which a gene substitution could produce a change in either direction depending upon the remaining genotype. In this respect, a one-locus model with overdominance would be irregular.

Several irregular models were constructed and tested for negative covariances. In addition to being irregular, these models have the common feature that the superior heterozygote is no better than the superior homozygote; therefore, fixation of the best genotype is possible by within-line selection. It was desirable to have some objective method for defining the epistatic models. If the occurrence of a negative covariance is related to the kinds of epistatic variance, then models differing in this respect should be investigated. With these prerequisites as a guide, the models in Table 1 were constructed. The three models AA, AD and DD were designed such that, when all gene frequencies in a population are $\frac{1}{2}$, the total genetic variance is equal to only one kind of epistatic variance: additive × additive (model AA), additive × dominance (model AD) or dominance × dominance (model DD). An additional feature of model AA is that the dominance, additive × dominance and dominance × dominance variances are zero, independent of gene frequencies.

The results of the covariance calculations are shown in Fig. 1 for all combinations of gene frequencies from 0·1 to 0·9 with increments of 0·1. The representation of Tester frequencies is not exact; there are slight variations of the actual location of negative covariances dependent upon the particular frequency combination

in the selected population. However, in general, this is an adequate portrayal of the covariance situation.

The results from these models demonstrate that negative covariances can occur even though no heterozygote is superior to all homozygotes. In all three models, negative covariances occur when the frequencies in Selected and in Tester tend to be divergent. In models AD and DD this is not as necessary as in model AA. That the range of gene frequency combinations allowing negative covariances is much

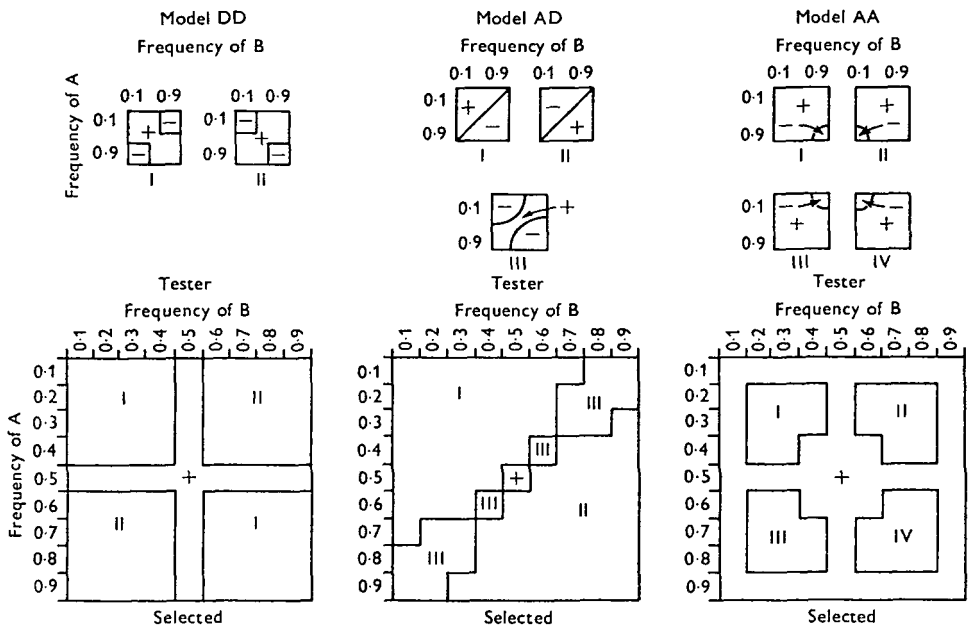

Fig. 1. Covariance for AA, AD and DD epistatic models. For a particular combination of A, B frequencies in the selected population a Roman numeral is provided to refer to a square above Tester which shows the sign of the covariance for A, B frequencies in the Tester. If a location in the Selected square provides a ' + ', then only non-negative covariances are obtained regardless of gene frequencies in the Tester.

smaller in AA than in AD and DD suggests that dominance types of epistatic variance are closely related to occurrence of negative covariances. Of course this cannot be a perfect relationship since negative covariances do occur with model AA for which all variances arising from dominance are zero.

Two additional models were compared to relate the degree of irregularity with the range of occurrence of negative covariances. These models, shown in Table 1, were obtained by changing two heterozygotes in an additive model. In model OD 1 the heterozygotes *Aabb* and *aaBb* were made superior to all other genotypes; in model OD 2 they were made superior only to their corresponding homozygotes. Thus model OD 1 has a higher degree of irregularity.

The results are presented in Fig. 2. The range of frequency combinations for

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which negative covariances are found is much larger for Model OD 1 than that for Model OD 2.

The models studied here have not been chosen as the only models which could yield the results obtained. Their objective selection was intended to demonstrate the conclusions reached and hopefully these models are representative of real possibilities. At the very least they fulfil the purpose of this paper.

Table 1. *Genotypic values for epistatic models*

Genotypic array for models	AABB AaBB aaBB	AABb AaBa aaBb	AAbb Aabb aabb
Model AA	8 4 0 4 4 4 0 4 8		
Model AD		8 2 4 2 4 6 4 6 0	
Model DD			6 4 6 4 6 4 6 4 6
Model OD 1	6 5 4 5 4 7 4 7 2		
Model OD 2		6 5 4 5 4 5 4 5 2	

3. DISCUSSION

The covariance technique proposed by Bowman (1960) was intended to detect overdominance. However, most authors have been sceptical of this technique because his model was limited to two alleles at a single locus. The results presented here using epistatic models demonstrate that their doubts were warranted. It must be concluded that a negative covariance does not necessarily imply heterozygote superiority. As a positive covariance may occur with overdominance for one-locus models so may a negative covariance occur without heterozygote superiority for epistatic models.

Irregular epistatic models appear necessary for producing negative covariances from two-locus models. The range of frequency combinations for which negative covariances are found seems to be closely related to the dominance types of epistatic variance. In all models, the gene frequencies should be divergent in the two populations to obtain a negative covariance.

Bowman (1960) argued that a plateaued line will tend to be fixed for those loci not exhibiting heterozygote superiority and will yield a negative pure bred–crossbred covariance due to the superiority of heterozygotes at segregating loci. However, if the line is plateaued because of exhaustion of additive genetic variance, then both additive and additive × additive effects are necessarily zero; consequently, the purebred–crossbred covariance automatically will also be zero.

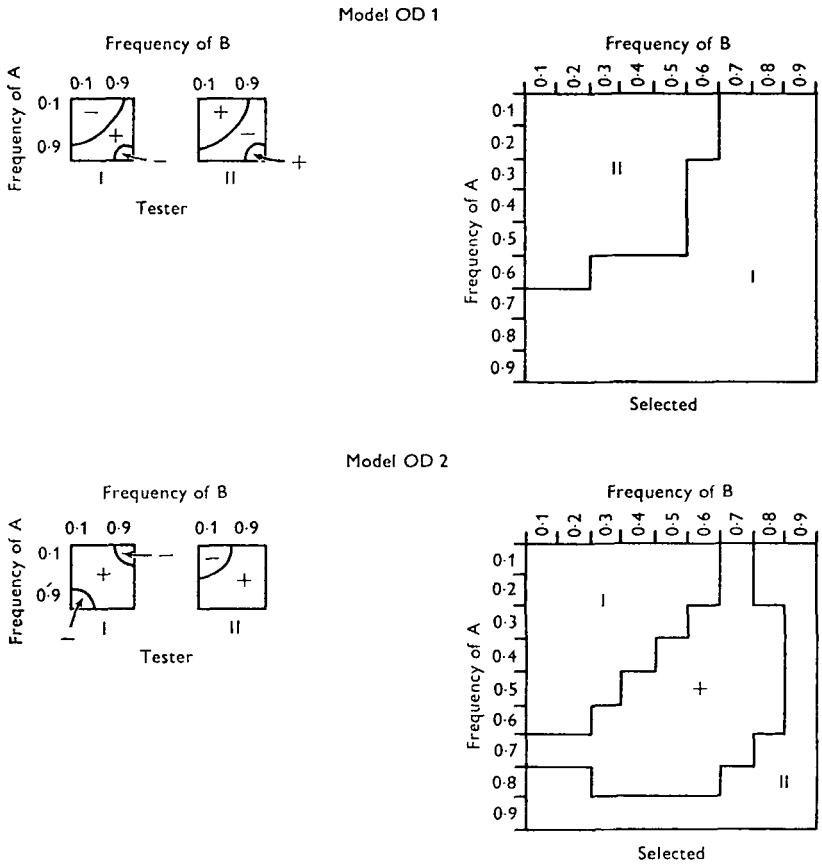

Fig. 2. Covariance for OD 1 and OD 2 epistatic models. For a particular combination of A, B frequencies in the Selected population, a Roman numeral is provided to refer to a square above Tester which shows the sign of the covariance for A, B frequencies in the Tester. If a location in the Selected square provides a '+', then only non-negative covariances are obtained regardless of gene frequencies in the Tester.

It is clear from this that a line must exhibit additive or additive × additive variance to permit a non-zero covariance.

Even though these considerations may limit inferences from a negative covariance, there is yet a sufficient reason for retaining the covariance as an analytic tool. It would appear from the examples presented here that, upon observing a negative covariance, one can justifiably conclude significant non-additivity of gene effects. This may be useful to the breeder in deciding on a selection method.

A relevant consequence of this study concerns the predictive value of the covariance. Griffing (1962) has determined expressions for the change in the purebred mean when selection is for crossbred performance and vice versa. The change is a function of the covariance under consideration in this paper and has the same sign as the covariance when the tester is not selected. Prediction, however, is only useful for short-term selection in which gene frequencies undergo small changes.

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In the sense of a selection limit, the sign cannot predict whether selection should be for purebred performance. Robinson, Louca & Legates (1964) found a negative covariance for litter number in swine and suggested that non-additive gene action was involved. They concluded that 'selection for purebred performance will be relatively ineffective for improving crossbreds'. While this statement is true for the short run, it should not be inferred that crossbred selection will lead to the maximum value. Selection in purebreds may yet produce the best possible genotype. Of course this presupposes that the necessary genes are present in the purebreds.

Table 2. *Purebred and crossbred means for model AD when A, B frequencies in Tester are 0·2 and 0·4 respectively*

Frequency of A	Frequency of B					
	0·0	0·2	0·4	0·6	0·8	1·0
0·0	0·00*	2·08	3·52	*4·32*	*4·48*	*4·00*
	2·96†	3·33	3·70	*4·06*	*4·43*	*4·80*
0·2	2·08	3·14	3·81	*4·10*	*4·00*	3·52
	3·33	3·57	3·81	*4·05*	*4·29*	*4·53*
0·4	3·52	3·81	3·97	*4·00*	3·90	3·68
	3·70	3·81	3·92	*4·03*	*4·14*	*4·26*
0·6	*4·32*	*4·10*	*4·00*	*4·00*	*4·19*	*4·48*
	4·06	*4·05*	*4·03*	*4·02*	*4·00*	3·98
0·8	*4·48*	*4·00*	3·90	*4·19*	*4·86*	*5·92*
	4·43	*4·29*	*4·14*	*4·00*	3·86	3·71
1·0	*4·00*	3·52	3·68	*4·48*	*5·92*	*8·00*
	4·80	*4·53*	*4·26*	3·98	3·71	3·44

* Upper value is purebred mean. † Lower value is crossbred mean.

An example of this possibility is provided by model AD. In a purebred line, three selective peaks occur: one each when either A or B alleles has frequency 0·0 and the other has frequency 0·75, and the third when both A and B are fixed. To which peak the population would move depends on the gene frequencies when selection is initiated.

Consider a particular example. In Table 2 are shown the means of the purebreds and crossbreds when Tester has allelic frequencies of 0·2 for A and 0·4 for B. Let Tester remain unselected and let the Selected Population have frequencies of 0·7 and 0·5 for A and B. The population means are: Tester, 3·81; Selected, 4·00; Crossbred, 4·05. Thus at the outset the crossbred is superior to both parental populations. Referring to Fig. 1 it will be seen that the covariance is negative. Thus selection in either the purebreds or crossbreds will move their means in opposite directions. However, selection in the crossbred approaches a limit of 4·8 while selection in the purebred approaches a limit of 8·0 or fixation of the best genotype. This example demonstrates that the covariance can be negative, the crossbred can be superior to both parents, and yet crossbred selection should not be used to fix

the best genotype. It should not be concluded from this statement that, if Tester were also selected for purebred performance, the maximum response would be obtained. If selection were practised in Tester, it would move to the peak with A at a frequency of 0·0 and B at a frequency of 0·75, as can be seen from Table 2. Thus neither Tester nor the crossbred would achieve the maximum genotype.

The purpose of this example is not to demonstrate any general result about various selection methods; rather, it is to show that the sign of the covariance may have limited use in predicting the best long-range method. For this particular example the only method which achieves the maximum is pure-line selection, even though the covariance was negative.

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