GENE EFFECTS AND VARIANCES IN HYBRID POPULATIONS[1]

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MOST of the developments in quantitative genetic theory focus on the study of intrapopulation concepts. With an increasing consideration of more divergent genetic materials, a need for theory relating to hybrid populations exists.

In this study two methods for characterizing the gene effects and genetic variability in interpopulation hybrids are compared. Also, covariances among relatives are compared for the two methods. The immediate interpopulation generated by crossing random individuals from two parent populations provides the reference base for defining the genetic parameters. Linkage equilibrium is assumed in each parent population so that gene distributions are uncorrelated in the reference populations.

Effects of genes defined according to origin: The genotypic model for a hybrid individual as a function of uniting gametes is

$$Y_{1_i 2_j} = \mu + g_{1_i} + g_{2_j} + s_{1_i 2_j} ,$$

where g_{1_i} denotes the effect of the ith gamete originating from population 1, g_{2_j} denotes the effect of the jth gamete originating from population 2, and $s_{1_i 2_j}$ represents an interaction effect. Since the gametes generating the hybrids are uncorrelated, the genotypic variance is simply

$$\sigma^2_Y = \sigma^2_{g_1} + \sigma^2_{g_2} + \sigma^2_{s_{12}} .$$

As given by GRIFFING (1962) and SCHNELL (1965), the model may be further subdivided into gene effects, and in this case for two loci, k and m,

$$g_{t_i} = \alpha^{(k)}_{(t_i)} + \alpha^{(m)}_{(t_{i'})} + \alpha\alpha^{(k)\ (m)}_{(t_i)(t_{i'})} \quad ; \quad (t = 1,2) \tag{1}$$

$$\begin{aligned} s_{1_i 2_j} = {} & \delta^{(k)}_{(1_i 2_j)} + \delta^{(m)}_{(1_{i'} 2_{j'})} + \left[\alpha\alpha^{(k)\ (m)}_{(1_i)(2_{j'})} + \alpha\alpha^{(k)\ (m)}_{(2_j)(1_{i'})}\right] \\ & + \left[\alpha\delta^{(k)\ (m)}_{(1_i)(1_{i'} 2_{j'})} + \alpha\delta^{(k)\ (m)}_{(1_i 2_j)(1_{i'})}\right] \\ & + \left[\alpha\delta^{(k)\ (m)}_{(2_j)(1_{i'} 2_{j'})} + \alpha\delta^{(k)\ (m)}_{(1_i 2_j)(2_{j'})}\right] + \delta\delta^{(k)\ (m)}_{(1_i 2_j)(1_{i'} 2_{j'})} . \end{aligned} \tag{2}$$

Even though the same alleles are contained in both populations, they have different effects unless the two parent populations are identical. For example, the ith allele, $a^{(k)}_{(i)}$, at locus k, has two additive effects, $\alpha^{(k)}_{(1_i)}$ and $\alpha^{(k)}_{(2_i)}$, one in each of the two types of gametic effects. Likewise, four types of additive by additive

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effects are defined for the ith and jth alleles, $a^{(k)}_{(i)}$ and $a^{(m)}_{(j')}$, at loci k and m, respectively.

Variances for similar types of gene effects also differ, with the genotypic variance being partitioned as follows:

$$\sigma^2_Y = \sigma^2_{A_1} + \sigma^2_{A_2} + \sigma^2_D + \sigma^2_{A_1A_1} + \sigma^2_{A_1A_2} + \sigma^2_{A_2A_2} + \sigma^2_{A_1D} + \sigma^2_{A_2D} + \sigma^2_{DD} + \sigma^2_{A_1A_1A_1} + \sigma^2_{A_1A_1A_2} + \sigma^2_{A_1A_2A_2} + \sigma^2_{A_2A_2A_2} + \sigma^2_{A_1A_1D} + \ldots, \tag{3}$$

where the subscripts, 1 and 2, designate the origin of the genes from the two parent populations. The extension to more than two loci as in (3) is straightforward. Explicit expressions for the variances for two loci, two alleles each, are given in Appendix B.

Effects of genes defined uniquely: Effects of genes in random mating populations normally are defined uniquely in a least squares sense (KEMPTHORNE 1955). If effects of genes are defined uniquely in a hybrid population, the genotypic model of a hybrid individual is the usual factorial one, which for two loci, k and m, is

$$\begin{aligned} \mathrm{Y}^{(k)\ (m)}_{(ii')(jj')} = \mu &+ \alpha^{(k)}_{(i)} + \alpha^{(k)}_{(i')} + \delta^{(k)}_{(ii')} + \alpha^{(m)}_{(j)} + \alpha^{(m)}_{(j')} \\ &+ \delta^{(m)}_{(jj')} + \alpha\alpha^{(k)(m)}_{(i)(j)} + \alpha\alpha^{(k)(m)}_{(i)(j')} + \alpha\alpha^{(k)\ (m)}_{(i')(j)} \\ &+ \alpha\alpha^{(k)\ (m)}_{(i')(j')} + \alpha\delta^{(k)(m)}_{(i)(jj')} + \alpha\delta^{(k)\ (m)}_{(i')(jj')} \\ &+ \alpha\delta^{(k)\ (m)}_{(ii')(j)} + \alpha\delta^{(k)\ (m)}_{(ii')(j')} + \delta\delta^{(k)\ (m)}_{(ii')(jj')} . \end{aligned} \tag{4}$$

For the unique effects model,

$$\sigma^2_Y = \sigma^2_{\underline{A}} + \sigma^2_{\underline{D}} + \sigma^2_{\underline{AA}} + \sigma^2_{\underline{AD}} + \sigma^2_{\underline{DD}} + \ldots . \tag{5}$$

The total genetic variance, σ^2_Y, is the same in (3) and (5); it is just partitioned differently.

Explicit expressions of the variances for two loci, two alleles each, are presented in Appendix C for the uniquely defined effects. Details for deriving these variances are given by STUBER (1965).

Since the model, (4), used in obtaining $\sigma^2_{\underline{A}}$ is a restriction of the model, (1), leading to $\sigma^2_{A_1}$ and $\sigma^2_{A_2}$, it should be obvious that

$$\sigma^2_{A_1} + \sigma^2_{A_2} \geq \sigma^2_{\underline{A}} . \tag{6}$$

Consequently, $\sigma^2_D \leq \sigma^2_{\underline{D}}$. The validity of (6) can be seen in the proof presented in Appendix D. For the epistatic variance components, the result is analogous with less variance attributed to the effects with only additive in their nomenclatures and more to the all dominance types of effects in the unique definitional system.

Covariances among Hybrid Relatives

The major differences between the two definitional systems lie in the expressions of the covariances among cross population relatives. For the dually defined effects, the covariances have almost the same simplicity as in a single random mating population. With the assumption of no linkages, the expectations can be expressed simply as

$$Cov = \Phi_1 \sigma^2_{A_1} + \Phi_2 \sigma^2_{A_2} + \Phi_1 \Phi_2 \sigma^2_D + \Phi_1^2 \sigma^2_{A_1A_1} + \Phi_2^2 \sigma^2_{A_2A_2} + \Phi_1 \Phi_2 \sigma^2_{A_1A_2} + \Phi_1^2 \Phi_2 \sigma^2_{A_1D} + \Phi_1 \Phi_2^2 \sigma_{A_2D} + \Phi_1^2 \Phi_2^2 \sigma^2_{DD} + \ldots , \quad (7)$$

where Φ_i denotes the probability that genes originating from population i are "identical by descent." For example, in the expectation of the covariance among half sibs with a common parent in population 1, $\Phi_1 = (1 + F_1)/2$ and $\Phi_2 = 0$ where F_1 denotes the coefficient of inbreeding of the parent in population 1. For the covariance among full sibs, $\Phi_1 = (1 + F_1)/2$ and $\Phi_2 = (1 + F_2)/2$.

Without linkage equilibrium, effects of genes at different loci are correlated in random mating populations. Similar, but more complex, correlations arise in hybrid populations when linkage equilibrium does not prevail in the parent populations. These correlated, nonallelic effects also appear in the covariances among relatives. Even with linkage equilibrium in the parent populations, the covariances among hybrid relatives are affected by linkages for which recombination values are less than 0.50. These linkage effects, which are analogous to those occurring in random mating populations, can be incorporated into the covariances for the dual definitional system. With the incorporation of linkage effects into (7), the coefficients, Φ_1 and Φ_2, remain unchanged. The Φ's raised to powers greater than one must be modified, however. SCHNELL (1965) presents a general formulation, including linkage effects, and gives expectations of covariances for several types of hybrid relatives.

Although the covariances among hybrid relatives do not vary with the definitional system, the formulations do vary and become much more complex when defined in terms of unique gene effects and variances. Correlations between many of the effects involve functions of gene frequencies. Consequently, the coefficients of the variance components in the covariance formulations depend not only on F, the inbreeding coefficient, but also on the frequencies of the genes at each locus in the two parent populations. Also, for many relatives, all types of effects are correlated. For example, additive effects in an individual are correlated with the dominance effects in a half-sib relative. Also, all types of two-factor epistatic effects are correlated for half sibs. STUBER (1965) presented the derivations of the covariances among half sibs and full sibs in detail for two alleles per locus and any number of loci.

DISCUSSION

More kinds of gene effects are distinguished for the definitional system based on the population of origin than for the unique definitional system. Correspondingly, more variance partitions exist for the dually defined effects. Formulations

of covariances among relatives in terms of genetic variances and gene effects defined according to origin are relatively simple when compared to the corresponding formulations in terms of unique gene effects and variances which involve complex functions of gene frequencies. Since the covariance formulations are elaborated more simply for the dual definitional system than for the unique system, procedures for estimating genetic variances are more straightforward for the former system.

The complexities associated with the unique definitional system arise because the genes at a locus are not in Hardy-Weinberg equilibrium. As a result, correlations exist between different types of gene effects for many relatives. The difficulties are similar to those associated with the translation of genetic variances among different generations of inbreeding. With only additive effects and additive types of epistasis in the model, the two definitional systems lead to the same variance partitions, i.e., $\sigma^2_{\bar{A}} = \sigma^2_{A_1} + \sigma^2_{A_2}$, $\sigma^2_{\bar{A}\bar{A}} = \sigma^2_{A_1A_1} + \sigma^2_{A_2A_2} + \sigma^2_{A_1A_2}$, and so on. However, even with this restricted model, the covariances among relatives for the unique system still involve complex functions of gene frequencies.

Interpretable relationships among effects and variances of the parent populations, the hybrid, and subsequent random mating generations would be desirable. Regardless of the definitional system, however, the variances cannot be directly related among generations because they are gene-frequency and gene-distribution dependent. For example, no variability arises in the parent populations or in the hybrid from loci at which different alleles are fixed in the two parent populations. These loci will contribute to the variation in subsequent random mating generations, however.

The additive variances associated with the two definitional systems do relate to different selection systems. The additive variance, $\sigma^2_{\bar{A}}$, assumes the same role in the formulation of progress from mass or full-sib family selection among the hybrids as the additive variance does for corresponding selection in a random mating population. The dual variances, $\sigma^2_{A_1}$ and $\sigma^2_{A_2}$, on the other hand, relate to progress from hybrid selection of the reciprocal recurrent type (COMSTOCK, ROBINSON, and HARVEY 1949). Since $\sigma^2_{A_1} + \sigma^2_{A_2} \geq \sigma^2_{\bar{A}}$, the advantage of reciprocal recurrent selection over mass and family selection among hybrids for the initial generation is apparent. Ordinarily, mass or family selection would not be initiated until after at least one generation of random mating in order to take advantage of the segregation of genes fixed or near fixation in the parent populations.

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SUMMARY

Genetic effects and variances in the F_1 of an interpopulation cross were compared for a dual and a unique definitional system. For the dual system the effects of genes are defined according to origin as opposed to the unique system of singly defined effects. Comparisons between the variance partitions for the two systems

showed that more variance is assigned to the all additive components and less variance is attributed to the all dominance components when the dual definitional system is used.—Covariances among relatives were also compared for the two definitional methods. These covariances have nearly the same simplicity for the dual definitional system as in a random mating population. For the unique system they are extremely complex with gene frequencies being involved in the coefficients of the variance components.

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APPENDIX A: GENETIC VALUES OF THE NINE GENOTYPES FOR TWO LOCI, EACH WITH TWO ALLELES

AABB	AABb	AAbb	AA__
Y_{22}	Y_{21}	Y_{20}	$Y_{2.}$
AaBB	AaBb	Aabb	Aa__
Y_{12}	Y_{11}	Y_{10}	$Y_{1.}$
aaBB	aaBb	aabb	aa__
Y_{02}	Y_{01}	Y_{00}	$Y_{0.}$
__BB	__Bb	__bb	
$Y_{.2}$	$Y_{.1}$	$Y_{.0}$	$Y_{..}$

APPENDIX B: PARTITIONS OF GENETIC VARIANCE IN THE INTERPOPULATION FOR TWO LOCI, EACH WITH TWO ALLELES, WHEN GENE EFFECTS ARE DEFINED ACCORDING TO ORIGIN*

$$\sigma^2_{A_1} = p^{(a)}_{(1)}(1-p^{(a)}_{(1)})\left[p^{(a)}_{(2)}(Y_{2.}-Y_{1.}) + (1-p^{(a)}_{(2)})(Y_{1.}-Y_{0.})\right]^2$$
$$+ p^{(b)}_{(1)}(1-p^{(b)}_{(1)})\left[p^{(b)}_{(2)}(Y_{.2}-Y_{.1}) + (1-p^{(b)}_{(2)})(Y_{.1}-Y_{.0})\right]^2$$

$$\sigma^2_{A_2} = p^{(a)}_{(2)}(1-p^{(a)}_{(2)})\left[p^{(a)}_{(1)}(Y_{2.}-Y_{1.}) + (1-p^{(a)}_{(1)})(Y_{1.}-Y_{0.})\right]^2$$
$$+ p^{(b)}_{(2)}(1-p^{(b)}_{(2)})\left[p^{(b)}_{(1)}(Y_{.2}-Y_{.1}) + (1-p^{(b)}_{(1)})(Y_{.1}-Y_{.0})\right]^2$$

$$\sigma^2_{D_{12}} = p^{(a)}_{(1)}p^{(a)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})\left[(Y_{2.}-Y_{1.}) - (Y_{1.}-Y_{0.})\right]^2$$
$$+ p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})\left[(Y_{.2}-Y_{.1}) - (Y_{.1}-Y_{.0})\right]^2$$

$$\sigma^2_{A_1A_1} = p^{(a)}_{(1)}p^{(b)}_{(1)}(1-p^{(a)}_{(1)})(1-p^{(b)}_{(1)})\left[p^{(a)}_{(2)}p^{(b)}_{(2)}e_{22} + p^{(a)}_{(2)}(1-p^{(b)}_{(2)})e_{21} + (1-p^{(a)}_{(2)})p^{(b)}_{(2)}e_{12} + (1-p^{(a)}_{(2)})(1-p^{(b)}_{(2)})e_{11}\right]^2$$

$$\sigma^2_{A_2A_2} = p^{(a)}_{(2)}p^{(b)}_{(2)}(1-p^{(a)}_{(2)})(1-p^{(b)}_{(2)})\left[p^{(a)}_{(1)}p^{(b)}_{(1)}e_{22} + p^{(a)}_{(1)}(1-p^{(b)}_{(1)})e_{21} + (1-p^{(a)}_{(1)})p^{(b)}_{(1)}e_{12} + (1-p^{(a)}_{(1)})(1-p^{(b)}_{(1)})e_{11}\right]^2$$

$$\sigma^2_{A_1A_2} = p^{(a)}_{(1)}p^{(b)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(b)}_{(2)})\left[p^{(a)}_{(2)}p^{(b)}_{(1)}e_{22} + p^{(a)}_{(2)}(1-p^{(b)}_{(1)})e_{21} + (1-p^{(a)}_{(2)})p^{(b)}_{(1)}e_{12} + (1-p^{(a)}_{(2)})(1-p^{(b)}_{(1)})e_{11}\right]^2$$
$$+ p^{(a)}_{(2)}p^{(b)}_{(1)}(1-p^{(a)}_{(2)})(1-p^{(b)}_{(1)})\left[p^{(a)}_{(1)}p^{(b)}_{(2)}e_{22} + p^{(a)}_{(1)}(1-p^{(b)}_{(2)})e_{21} + (1-p^{(a)}_{(1)})p^{(b)}_{(2)}e_{12} + (1-p^{(a)}_{(1)})(1-p^{(b)}_{(2)})e_{11}\right]^2$$

$$\sigma^2_{A_1D} = p^{(a)}_{(1)}p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})\left[p^{(a)}_{(2)}(e_{22}-e_{21}) + (1-p^{(a)}_{(2)})(e_{12}-e_{11})\right]^2$$
$$+ p^{(a)}_{(1)}p^{(a)}_{(2)}p^{(b)}_{(1)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(1-p^{(b)}_{(1)})\left[p^{(b)}_{(2)}(e_{22}-e_{12}) + (1-p^{(b)}_{(2)})(e_{21}-e_{11})\right]^2$$

$$\sigma^2_{A_2D} = p^{(a)}_{(2)}p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(a)}_{(2)})(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})\left[p^{(a)}_{(1)}(e_{22}-e_{21}) + (1-p^{(a)}_{(1)})(e_{12}-e_{11})\right]^2$$
$$+ p^{(a)}_{(1)}p^{(a)}_{(2)}p^{(b)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(1-p^{(b)}_{(2)})\left[p^{(b)}_{(1)}(e_{22}-e_{12}) + (1-p^{(b)}_{(1)})(e_{21}-e_{11})\right]^2$$

$$\sigma^2_{DD} = p^{(a)}_{(1)}p^{(a)}_{(2)}p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})\left[e_{22}-e_{21}-e_{12}+e_{11}\right]^2$$

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*$p^{(a)}_{(1)}$ and $p^{(b)}_{(1)}$ denote the frequencies of A and B in population 1, respectively. Likewise, $p^{(a)}_{(2)}$ and $p^{(b)}_{(2)}$ denote the frequencies in population 2.

$e_{22} = Y_{22} - Y_{21} - Y_{12} + Y_{11}$; $e_{21} = Y_{21} - Y_{20} - Y_{11} + Y_{10}$;

$e_{12} = Y_{12} - Y_{11} - Y_{02} + Y_{01}$; $e_{11} = Y_{11} - Y_{10} - Y_{01} + Y_{00}$.

Y's refer to genetic values given in Appendix A.

APPENDIX C: PARTITIONS OF GENETIC VARIANCE IN THE INTERPOPULATION FOR TWO LOCI, EACH WITH TWO ALLELES, WHEN GENE EFFECTS ARE DEFINED UNIQUELY*

$$\sigma^2_{\bar{A}} = \frac{\left[p^{(a)}_{(1)}p^{(a)}_{(2)}(2-p^{(a)}_{(1)}-p^{(a)}_{(2)})(Y_{2.}-Y_{1.})+(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(p^{(a)}_{(1)}+p^{(a)}_{(2)})(Y_{1.}-Y_{0.})\right]^2}{T^{(a)}}$$

$$+ \frac{\left[p^{(b)}_{(1)}p^{(b)}_{(2)}(2-p^{(b)}_{(1)}-p^{(b)}_{(2)})(Y_{.2}-Y_{.1})+(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})(p^{(b)}_{(1)}+p^{(b)}_{(2)})(Y_{.1}-Y_{.0})\right]^2}{T^{(b)}}$$

$$\sigma^2_{\bar{D}} = \frac{p^{(a)}_{(1)}p^{(a)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})H^{(a)}\left[(Y_{2.}-Y_{1.})-(Y_{1.}-Y_{0.})\right]^2}{T^{(a)}}$$

$$+ \frac{p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})H^{(b)}\left[(Y_{.2}-Y_{.1})-(Y_{.1}-Y_{.0})\right]^2}{T^{(b)}}$$

$$\sigma^2_{\bar{A}\bar{A}} = \frac{\left\{p^{(a)}_{(1)}p^{(a)}_{(2)}(2-p^{(a)}_{(1)}-p^{(a)}_{(2)})\left[p^{(b)}_{(1)}p^{(b)}_{(2)}(2-p^{(b)}_{(1)}-p^{(b)}_{(2)})e_{22}+(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})(p^{(b)}_{(1)}+p^{(b)}_{(2)})e_{21}\right]\right.}{\left.+(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(p^{(a)}_{(1)}+p^{(a)}_{(2)})\left[p^{(b)}_{(1)}p^{(b)}_{(2)}(2-p^{(b)}_{(1)}-p^{(b)}_{(2)})e_{12}+(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})(p^{(b)}_{(1)}+p^{(b)}_{(2)})e_{11}\right]\right\}^2}{T^{(a)}\,T^{(b)}}$$

$$\sigma^2_{\bar{A}\bar{D}} = \frac{\left\{\begin{array}{l} p^{(a)}_{(1)}p^{(a)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})H^{(a)}\left[p^{(b)}_{(1)}p^{(b)}_{(2)}(2-p^{(b)}_{(1)}-p^{(b)}_{(2)})(e_{22}-e_{12})\right. \\ \left.+(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})(p^{(b)}_{(1)}+p^{(b)}_{(2)})(e_{21}-e_{11})\right]^2 \\ +\,p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})H^{(b)}\left[p^{(a)}_{(1)}p^{(a)}_{(2)}(2-p^{(a)}_{(1)}-p^{(a)}_{(2)})(e_{22}-e_{21})\right. \\ \left.+(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(p^{(a)}_{(1)}+p^{(a)}_{(2)})(e_{12}-e_{11})\right]^2 \end{array}\right\}}{T^{(a)}\,T^{(b)}}$$

$$\sigma^2_{\bar{D}\bar{D}} = \frac{p^{(a)}_{(1)}p^{(a)}_{(2)}p^{(b)}_{(1)}p^{(b)}_{(2)}(1-p^{(a)}_{(1)})(1-p^{(a)}_{(2)})(1-p^{(b)}_{(1)})(1-p^{(b)}_{(2)})H^{(a)}H^{(b)}(e_{22}-e_{21}-e_{12}+e_{11})^2}{T^{(a)}\,T^{(b)}}$$

*$p^{(a)}_{(1)}$ and $p^{(b)}_{(1)}$ denote the frequencies of A and B in population 1, respectively. Likewise, $p^{(a)}_{(2)}$ and $p^{(b)}_{(2)}$ denote the frequencies in population 2.

$T^{(a)} = 2\bar{p}^{(a)}(1-\bar{p}^{(a)}) - (\Delta^{(a)})^2/_2$ and $H^{(a)} = 2\bar{p}^{(a)}(1-\bar{p}^{(a)}) + (\Delta^{(a)})^2/_2$,

where $\bar{p}^{(a)} = (p^{(a)}_{(1)} + p^{(a)}_{(2)})/2$ and $\Delta^{(a)} = p^{(a)}_{(1)} - p^{(a)}_{(2)}$.

$e_{22} = Y_{22} - Y_{21} - Y_{12} + Y_{11}$; $e_{21} = Y_{21} - Y_{20} - Y_{11} + Y_{10}$;

$e_{12} = Y_{12} - Y_{11} - Y_{02} + Y_{01}$; $e_{11} = Y_{11} - Y_{10} - Y_{01} + Y_{00}$.

Y's refer to genetic values given in Appendix A.

APPENDIX D: PROOF THAT $\sigma^2_{A_1} + \sigma^2_{A_2} \geq \sigma^2_{A}$

In the unique definitional system, model (4), a single least squares effect is defined for the ith allele at the kth locus, $a^{(k)}_{(i)}$. This effect may be expressed as a function of the two effects, $\alpha^{(k)}_{(1_i)}$ and $\alpha^{(k)}_{(2_i)}$, defined for the dual system,

$$\alpha^{(k)}_{(i)} = \bar{\alpha}^{(k)}_{(i)} + \frac{\Delta^{(k)}_{(i)}\bar{t}^{(k)}}{4\bar{p}^{(k)}_{(i)}}$$

where

$$\bar{\alpha}^{(k)}_{(i)} = \frac{p^{(k)}_{(1_i)}\alpha^{(k)}_{(1_i)} + p^{(k)}_{(2_i)}\alpha^{(k)}_{(2_i)}}{2\bar{p}^{(k)}_{(i)}}, \quad \Delta^{(k)}_{(i)} = p^{(k)}_{(1_i)} - p^{(k)}_{(2_i)},$$

$$\bar{t}^{(k)} = \frac{\sum_i w^{(k)}_{(i)} t^{(k)}_{(i)}}{\sum_i w^{(k)}_{(i)}}, \quad w^{(k)}_{(i)} = \frac{p^{(k)}_{(1_i)} p^{(k)}_{(2_i)}}{2\bar{p}^{(k)}_{(i)}},$$

$$t^{(k)}_{(i)} = \alpha^{(k)}_{(2_i)} - \alpha^{(k)}_{(1_i)}, \text{ and } \bar{p}^{(k)}_{(i)} = \frac{p^{(k)}_{(1_i)} + p^{(k)}_{(2_i)}}{2}.$$

Thus, $\bar{\alpha}^{(k)}_{(i)}$ is a weighted average of the effects, $\alpha^{(k)}_{(1_i)}$ and $\alpha^{(k)}_{(2_i)}$. Also, $\bar{t}^{(k)}$, which is a constant for the kth locus, is a weighted average of the differences, $\alpha^{(k)}_{(2_i)} - \alpha^{(k)}_{(1_i)}$.

With the restriction that

$$\sum_i \bar{p}^{(k)}_{(i)}\alpha^{(k)}_{(i)} = 0,$$

the additive variance associated with the uniquely defined effects for the kth locus is

$$\sigma^{2(k)}_{\alpha} = 2\sum_i \bar{p}^{(k)}_{(i)}\left[\alpha^{(k)}_{(i)}\right]^2 + 2\left[\sum_i p^{(k)}_{(1_i)}\alpha^{(k)}_{(i)}\right]\left[\sum_i p^{(k)}_{(2_i)}\alpha^{(k)}_{(i)}\right]$$

When compared with the additive variance attributed to the dually defined effects, the following difference is obtained:

$$d^{(k)}_{\alpha} = \left[\sigma^{2(k)}_{\alpha_{(1)}} + \sigma^{2(k)}_{\alpha_{(2)}}\right] - \sigma^{2(k)}_{\alpha} = \sum_i w^{(k)}_{(i)}\left[t^{(k)}_{(i)} - \bar{t}^{(k)}\right]^2,$$

a weighted sum of squares which is positive. This difference is included in the dominance variance. Thus,

$$\sigma^{2(k)}_{\delta} = \sigma^{2(k)}_{\delta_{(12)}} + d^{(k)}_{\alpha},$$

which results in the assignment of less variance to average effects of genes and more to the dominance deviations when the effects are defined uniquely.