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The Use of Matrix Specifications in Defining Gene Action in Genotypic Value Models and Generation Mean Analysis

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Summary. Gene action and interaction have been defined in the literature by the use of a variety of notations (Mather 1949; Hayman 1954, 1955, 1957; Jinks 1954; Kempthorne 1954, 1955). This leads to unnecessary complications in understanding the subject. This paper provides a simple convenient way of translating one parameterization into another and illustrates the simple linear relationship between them. The various notations are written in matrix form by the use of a specification matrix. This provides a convenient compact method of presentation of the relevant Equations. The linear relationship between the genetic parameters enables these to be estimated in the most convenient way and then converted to other parameters for the purposes of comparison. The generation means Equations of Hayman (1958) are derived using the matrix formulation as an illustration of the use of the specification matrix.

Key words: Generation means – Matrices – Genetics – Models

The Genotypic Value Model

The genetic effects for a locus with two alleles may be analysed in terms of the difference between the contrasting homozygotes and the deviation of the heterozygote from the mean of the homozygotes (Falconer 1970). This then defines the parameters m, a and d in terms of the genotypic values when considering two alleles, A_1 and A_2, at one locus:

$$\left.\begin{aligned} m &= (A_1A_1 + A_2A_2)/2 \\ a &= (A_1A_1 - A_2A_2)/2 \\ d &= (A_1A_2 - (A_1A_1 + A_2A_2)/2 \end{aligned}\right\} \quad (1)$$

Both the genotypes and the genotypic values are represented by use of the same notation but it is usually clear from the context which one is being referred to. In this model:
(i) 'a' represents the additive effect and must be a positive quantity as A_1A_1 is considered to be the homozygote which increases the manifestation of the character;
(ii) 'd' represents the dominance effect and can be either positive, negative, or zero.

The extension to the digenic case is achieved by considering two genes, A and B, each with two alleles. An additive-dominance model applies to each locus so, as discussed above, the parameters a_A, d_A, a_B and d_B may be defined in terms of the genotypic values. The subscript denotes the gene from which the effect is obtained. Four types of non-allelic interaction or epistasis are possible and may be defined as follows:

$$\left.\begin{aligned} aa_{AB} &= a_Aa_B && \text{(additive × additive)} \\ ad_{AB} &= a_Ad_B \\ ad_{BA} &= a_Bd_A && \text{(additive × dominance)} \\ dd_{AB} &= d_Ad_B && \text{(dominance × dominance)} \end{aligned}\right\} \quad (2)$$

These parameters are used to analyse the genetic effects observable from the nine possible genotypes. To give a complete description, a ninth parameter m is defined as the mean of all four homozygotes in equal frequency:

$$m = (A_1A_1B_1B_1 + A_1A_1B_2B_2 + A_2A_2B_1B_1 + A_2A_2B_2B_2)/4 \quad (3)$$

This value would be the mean of the infinite generation of selfing denoted by F_∞ (Mather and Jinks 1971).

It is possible to define mathematically the genotypic specification by use of matrix algebra. Consider the Equation:

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$$\mathbf{S}\underset{\sim}{g} = \underset{\sim}{v} \tag{4}$$

where

$\mathbf{S}$ = 9 × 9 specification matrix,

$\underset{\sim}{g}$ = 9 × 1 parameter vector,

$\underset{\sim}{v}$ = 9 × 1 vector of measured genotypic values.

To illustrate this, consider the digenic model discussed by Mather and Jinks (1971). Equation 4 for this specification is written as follows:

$$\begin{bmatrix} 1 & 1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 0 \\ 1 & 1 & -1 & 0 & 0 & -1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 0 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & -1 & 1 & 0 & 0 & 0 & -1 & 0 \\ 1 & -1 & 1 & 0 & 0 & -1 & 0 & 0 & 0 \\ 1 & -1 & 0 & 0 & 1 & 0 & -1 & 0 & 0 \\ 1 & -1 & -1 & 0 & 0 & 1 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} m \\ a_A \\ a_B \\ d_A \\ d_B \\ aa_{AB} \\ ad_{AB} \\ ad_{BA} \\ dd_{AB} \end{bmatrix} = \begin{bmatrix} A_1A_1B_1B_1 \\ A_1A_1B_1B_2 \\ A_1A_1B_2B_2 \\ A_1A_2B_1B_1 \\ A_1A_2B_1B_2 \\ A_1A_2B_2B_2 \\ A_2A_2B_1B_1 \\ A_2A_2B_1B_2 \\ A_2A_2B_2B_2 \end{bmatrix} \tag{5}$$

Although the right hand side of Eq. 4 will not change for a particular family, it is possible to vary $\mathbf{S}$ and hence $\underset{\sim}{g}$. $\mathbf{S}$ is defined in a particular way so that the parameters in $\underset{\sim}{g}$ have genetical meaning. Thus Eq. 4 should be written in the general form:

$$\mathbf{S}^{(j)}\underset{\sim}{g}^{(j)} = \underset{\sim}{v} \tag{6}$$

where j denotes a particular specification matrix and a particular parameter vector. Thus the relationship between any two parameter vectors can be considered as follows:

$$\mathbf{S}^{(j)}\underset{\sim}{g}^{(j)} = \mathbf{S}^{(k)}\underset{\sim}{g}^{(k)}$$

$$\underset{\sim}{g}^{(j)} = (\mathbf{S}^{(j)})^{-1}\mathbf{S}^{(k)}\underset{\sim}{g}^{(k)} \tag{7}$$

Any specification $\mathbf{S}^{(k)}$ may be used in solving Eq. 6 for $\underset{\sim}{v}$, and the parameter estimates ($\underset{\sim}{g}^{(k)}$) obtained may be interpreted, using Eq. 7, in terms of parameters of known genetical meaning. It follows that the specification matrix used could be the one which is most facile in the mathematical sense.

For many specific types of families or populations, the expected frequency distribution of the genotypes is known. A detailed discussion of these is given in Mather and Jinks (1971). A proportion matrix $\mathbf{P}$ may be defined such that each row denotes the expected frequency distribution of the nine possible genotypes present in a particular family in terms of the proportions of the family size. Then:

$$\mathbf{P} = \begin{bmatrix} \underset{\sim}{p}^{1\prime} \\ \vdots \\ \underset{\sim}{p}^{i\prime} \\ \vdots \\ \underset{\sim}{p}^{n\prime} \end{bmatrix} \tag{8}$$

where the superscript i refers to the i^{th} of the n observed families.

Some examples of these vectors for a digenic model are now given. Depending on whether the genes are associated or dispersed, the $\underset{\sim}{p}^{i\prime}$ for inbred lines would be defined as:

$$\left.\begin{array}{lll} \text{PA1} & : & (1\ 0\ 0\ \ 0\ 0\ 0\ \ 0\ 0\ 0) \\ \text{PA2} & : & (0\ 0\ 0\ \ 0\ 0\ 0\ \ 0\ 0\ 1) \\ \text{PD1} & : & (0\ 0\ 1\ \ 0\ 0\ 0\ \ 0\ 0\ 0) \\ \text{PD2} & : & (0\ 0\ 0\ \ 0\ 0\ 0\ \ 1\ 0\ 0) \end{array}\right\} \tag{9}$$

where PA1 and PD1 name the proportional row vectors referring to parent 1 with the genes in associated and dispersed state, respectively. Regardless of which of these types are used as parents, the F_1 and subsequent generations resulting from selfing the F_1 will have the same proportion vector $\underset{\sim}{p}^{i\prime}$ given by:

$$\left.\begin{array}{lll} F_1 & : & (0\ 0\ 0\ \ 0\ 1\ 0\ \ 0\ 0\ 0) \\ F_2 & : & (1\ 2\ 1\ \ 2\ 4\ 2\ \ 1\ 2\ 1)/16 \\ F_3 & : & (9\ 6\ 9\ \ 6\ 4\ 6\ \ 9\ 6\ 9)/64 \\ F_\infty & : & (1\ 0\ 1\ \ 0\ 0\ 0\ \ 1\ 0\ 1)/4 \end{array}\right\} \tag{10}$$

The backcross families depend on the original parent type. Their proportion vectors $\underset{\sim}{p}^{i\prime}$ are given as follows:

$$\left.\begin{array}{lll} \text{BCPA1} & : & (1\ 1\ 0\ \ 1\ 1\ 0\ \ 0\ 0\ 0)/4 \\ \text{BCPA2} & : & (0\ 0\ 0\ \ 0\ 1\ 1\ \ 0\ 1\ 1)/4 \\ \text{BCPD1} & : & (0\ 1\ 1\ \ 0\ 1\ 1\ \ 0\ 0\ 0)/4 \\ \text{BCPD2} & : & (0\ 0\ 0\ \ 1\ 1\ 0\ \ 1\ 1\ 0)/4 \end{array}\right\} \tag{11}$$

where BCPA1 and BCPD1 name the proportional row vectors referring to the backcross of the F_1 with parent 1 with the genes in associated and dispersed state, respectively. Vectors of this type are well known and the appropriate ones are chosen to form $\mathbf{P}$.

Thus the Equation:

$$\mathbf{PS}\underset{\sim}{g} = \mathbf{P}\underset{\sim}{v} \tag{12}$$

would have as the i^{th} element of the vector on the right hand side, the mean μ_i of the quantitative character over the different genotypes for the i^{th} family. This information could be more clearly represented as follows:

$$\mathbf{K}\underset{\sim}{g} = \underset{\sim}{\mu} \tag{13}$$

where

$\mathbf{K}$ = n × 9 known matrix given the inferred proportion vectors $\underset{\sim}{p}^i$ for each of n populations,

$\underset{\sim}{g}$ = 9 × 1 parameter vector,

$\underset{\sim}{\mu}$ = n × 1 vector of observed population means.

A simplification of the notation is now introduced by summing the effects over the two loci. Let:

$$[d] = d_A + d_B \tag{14}$$

As discussed earlier, d_A and d_B may be either positive, negative or zero so [d] may be either positive, negative or zero. However, a_A and a_B have been defined as positive quantities. If the increasing or decreasing alleles of the two genes are associated as in $A_1A_1B_1B_1$ or $A_2A_2B_2B_2$ then the resulting additive effect will be $(a_A + a_B)$ or $-(a_A + a_B)$. Conversely, if the alleles are dispersed, the additive effect will be $(a_A - a_B)$ or $-(a_A - a_B)$. Thus it will be supposed that the resulting additive effect when two genes are acting is:

$$[a] = \begin{cases} a_A + a_B, \text{ genes associated} \\ a_A - a_B, \text{ genes dispersed} \end{cases} \tag{15}$$

where it is assumed that:

$$a_A \geqslant a_B \tag{16}$$

so than [a] will be a positive quantity (or zero) as in the single gene case. Defining:

$$[ad] = \begin{cases} ad_{AB} + ad_{BA}, \text{ genes associated,} \\ ad_{AB} - ad_{BA}, \text{ genes dispersed,} \end{cases} \tag{17}$$

gives the corresponding definition to Eq. 15 for the resulting additive × dominance interaction. Also define:

$$\left.\begin{aligned} [aa] &= aa_{AB} \\ [dd] &= dd_{AB} \end{aligned}\right\} \tag{18}$$

The parameter vector $\underset{\sim}{g}$ is now defined as:

$$\underset{\sim}{g}' = (m\ [a]\ [d]\ [aa]\ [ad]\ [dd]) \tag{19}$$

Incorporating this into Eq. 13 gives:

$$\mathbf{K}\underset{\sim}{g} = \underset{\sim}{\mu} \tag{20}$$

where

$\mathbf{K}$ = n × 6 matrix of inferred proportion vectors for each of n families

$\underset{\sim}{g}$ = 6 × 1 parameters vector,

$\underset{\sim}{\mu}$ = n × 1 vector of observed population means.

The general form of Eq. 13 and 20 has $\underset{\sim}{g}$ as a q × 1 parameter vector and $\mathbf{K}$ an n × q matrix.

Considering the families discussed in Eq. 9-11, Eq. 20 would reduce to the following form:

$$\begin{bmatrix} 1 & 1 & 0 & 1 & 0 & 0 \\ 1 & -1 & 0 & 1 & 0 & 0 \\ 1 & 1 & 0 & -1 & 0 & 0 \\ 1 & -1 & 0 & -1 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 1 \\ 1 & 0 & \frac{1}{2} & 0 & 0 & \frac{1}{4} \\ 1 & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{16} \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & \frac{1}{2} & \frac{1}{2} & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} \\ 1 & -\frac{1}{2} & \frac{1}{2} & \frac{1}{4} & -\frac{1}{4} & \frac{1}{4} \\ 1 & \frac{1}{2} & \frac{1}{2} & -\frac{1}{4} & \frac{1}{4} & \frac{1}{4} \\ 1 & -\frac{1}{2} & \frac{1}{2} & -\frac{1}{4} & -\frac{1}{4} & \frac{1}{4} \end{bmatrix} \begin{bmatrix} m \\ [a] \\ [d] \\ [aa] \\ [ad] \\ [dd] \end{bmatrix} = \begin{bmatrix} \mu_{PA1} \\ \mu_{PA2} \\ \mu_{PD1} \\ \mu_{PD2} \\ \mu_{F_1} \\ \mu_{F_2} \\ \mu_{F_3} \\ \mu_{F_\infty} \\ \mu_{BCPA1} \\ \mu_{BCPA2} \\ \mu_{BCPD1} \\ \mu_{BCPD2} \end{bmatrix} \tag{21}$$

Note that either the combination of parents PA1 with PA2 or PD1 with PD2 is valid. The only difference between the two models is the sign of [aa]. Hence, only the first model is fitted and rows 3, 4, 11 and 12 of Eq. 21 are omitted. If [aa] is positive then the genes in the parents are associated and if [aa] is negative then the genes in the parents are dispersed.

Extension to the Polygenic Case

In extending to the polygenic case, Hayman and Mather (1955) felt there was little justification for considering any more complex interactions than the digenic ones until this type had been fully explored. For a quantitative continuously distributed character, it is impossible to isolate the effect of a particular gene, and the genotype of any particular individual is unknown. Performance represents the joint action and interaction of all gene effects contributing to that character. Thus no inferences about particular genes or gene effects can be made by studying individuals when dealing with truly quantitative traits.

The Equations considered above may be extended to

the polygenic case by use of the following general definitions:

$$\left.\begin{aligned} m &= \text{mean of homozygotes} \\ [a] &= \sum_i a_i \\ [d] &= \sum_i d_i \end{aligned}\right\} \quad (22)$$

and

$$\left.\begin{aligned} [aa] &= \sum_{\substack{i,j \\ i \neq j}} \longleftarrow aa_{ij} \\ [ad] &= \sum_{\substack{i,j \\ i \neq j}} \longleftarrow ad_{ij} \\ [dd] &= \sum_{\substack{i,j \\ i \neq j}} \longleftarrow dd_{ij} \end{aligned}\right\} \quad (23)$$

Generation Mean Analysis

Suppose that n families are being considered in a generation means analysis (Hayman 1958) and that $n \geqslant q$, the number of parameters being estimated. In Eq. 20 above, q = 6 as the full digenic model is being considered but if only main effects are considered then q = 3. For each family with an inferred proportion vector for the genotypes, the mean and variance of the mean within the family may be estimated and denoted by $\hat{\mu}_i$ and $\hat{\sigma}_i^2$, respectively. Provided the experimental design avoids correlations between the estimates $\hat{\mu}_i$, the variance-covariance matrix of $\underset{\sim}{\hat{\mu}}$ may be considered to be a diagonal matrix, **D**, with the error variances $\hat{\sigma}_i^2$ of each family mean down the diagonal. Then the least squares estimate of $\underset{\sim}{g}$ is obtained as:

$$\underset{\sim}{\hat{g}} = (\mathbf{K}'\mathbf{D}^{-1}\mathbf{K})^{-1}\mathbf{K}'\mathbf{D}^{-1}\underset{\sim}{\hat{\mu}} \quad (24)$$

with the variances and coveriances of the estimates given by:

$$\mathbf{V}(\underset{\sim}{\hat{g}}) = (\mathbf{K}'\mathbf{D}^{-1}\mathbf{K})^{-1} \quad (25)$$

A goodness-of-fit of the model is performed by calculating:

$$\chi^2_{n-q} = \underset{\sim}{\hat{\mu}}'\mathbf{D}^{-1}\underset{\sim}{\hat{\mu}} - \underset{\sim}{\hat{\mu}}'\mathbf{D}^{-1}\mathbf{K}\underset{\sim}{\hat{g}} \quad (26)$$

Equations 24-26 are given by Hayman (1958) but are now extended to consider an alternative parameter vector from the one that has been estimated. This desired parameter vector, $\underset{\sim}{\hat{g}}^{(j)}$, for example, can be calculated by using transformation Eq. 7 on the calculated parameter vector $\underset{\sim}{\hat{g}}^{(k)}$.

This gives:

$$\underset{\sim}{\hat{g}}^{(j)} = (\mathbf{S}^{(j)})^{-1}\mathbf{S}^{(k)}\underset{\sim}{\hat{g}}^{(k)} \quad (27)$$

and

$$\mathbf{V}(\underset{\sim}{\hat{g}}^{(j)}) = (\mathbf{S}^{(j)})^{-1}\mathbf{S}^{(k)}\mathbf{V}(\underset{\sim}{\hat{g}}^{(k)})(\mathbf{S}^{(k)})'((\mathbf{S}^{(j)})^{-1})' \quad (28)$$

Both these Equations can only be calculated if **S** is a square matrix of the same size as the parameter vector $\underset{\sim}{\hat{g}}$. If the additive-dominance model is being considered then $\underset{\sim}{\hat{g}}$ is a 3 × 1 vector and **S** is a 3 × 3 matrix so both Eq. 27 and 28 can be calculated.

If $\underset{\sim}{\hat{g}}$ is a 6 × 1 vector but **S** is a 9 ×9 matrix then use must be made of the transformation matrix which is equivalent to the summation notation introduced in Eq. 22 and 23. For the digenic case the transformation matrix **T** which reparameterizes the vector $\underset{\sim}{g}$ is as follows:

$$\mathbf{T} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad (29)$$

An additional matrix $\mathbf{T}^-$ which satisfies $\mathbf{T}\mathbf{T}^- = \mathbf{I}$ is required. It may be calculated by replacing the non-zero elements in each row of **T** by elements whose row sum equals 1 and transposing. One such $\mathbf{T}^-$ is:

$$\mathbf{T}^- = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{2} & 0 & 0 & 0 & 0 \\ 0 & \frac{1}{2} & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad (30)$$

Then for $\mathbf{S}^{(j)}$ and $\mathbf{S}^{(k)}$ both 9 × 9 matrices but $\underset{\sim}{\hat{g}}^{(j)}$ and $\underset{\sim}{\hat{g}}^{(k)}$ both 6 × 1 parameter vectors the required transformation Equations are:

$$\underset{\sim}{\hat{g}}^{(j)} = \mathbf{T}(\mathbf{S}^{(j)})^{-1}\mathbf{S}^{(k)}\mathbf{T}^-\underset{\sim}{\hat{g}}^{(k)} \quad (31)$$

and

$$\mathbf{V}(\underset{\sim}{\hat{g}}^{(j)}) = \mathbf{T}(\mathbf{S}^{(j)})^{-1}\,\mathbf{S}^{(k)}\,\mathbf{T}^{-}\mathbf{V}(\underset{\sim}{\hat{g}}^{(k)})\,(\mathbf{T}^{-})'\,(\mathbf{S}^{(k)})'\,(\mathbf{S}^{(j)})^{-1})'\,\mathbf{T}' \tag{32}$$

Thus the choice of a specification matrix and parameter vector is a matter of convenience. If the estimates of another parameter vector and its variance co-variance matrix are required then they can be obtained by using Eq. 31 and 32.

The matrix specifications and parameter vectors defined by several sources for a simple genotypic value model are compared in Table 1. The suggested standard notations given in the table are made to avoid confusion and to make them all compatible to one another. All are directly extendible to higher order epistatic terms. The changed notation for Hayman's model is simply to avoid confusion with the m and d values in Fisher's parameter vector. Thus, by using transformation Eq. 7, it is found that in relation to Fisher's parameter vector:

$$\left.\begin{aligned} M &= m + \frac{d}{2} \\ A &= a \\ D &= \frac{d}{2} \end{aligned}\right\} \tag{33}$$

and

$$\left.\begin{aligned} \mu &= m + \frac{d}{2} \\ \alpha &= \frac{a}{2} \\ \delta &= -\frac{d}{2} \end{aligned}\right\} \tag{34}$$

Table 1. Specification matrices for four commonly used definitions of genetical parameters with their associated notations

Source	Specification matrix	Parameter vector notation	Suggested parameter vector notation
Fisher (1918) Mather and Jinks (1971)	$\begin{pmatrix} 1 & 1 & 0 \\ 1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix}$	$\begin{pmatrix} m \\ a \\ d \end{pmatrix}^{a} \begin{pmatrix} m \\ d \\ h \end{pmatrix}^{b}$	$\begin{pmatrix} m \\ a \\ d \end{pmatrix}$
Hayman (1958)	$\begin{pmatrix} 1 & 1 & -1 \\ 1 & 0 & 1 \\ 1 & -1 & -1 \end{pmatrix}$	$\begin{pmatrix} m \\ d \\ h \end{pmatrix}$	$\begin{pmatrix} M \\ A \\ D \end{pmatrix}$
Kempthorne (1955, 1957)	$\begin{pmatrix} 1 & 2 & 1 \\ 1 & 0 & -1 \\ 1 & -2 & 1 \end{pmatrix}$	$\begin{pmatrix} \mu \\ \alpha \\ \alpha\alpha \end{pmatrix}$	$\begin{pmatrix} \mu \\ \alpha \\ \delta \end{pmatrix}$

[a] Fisher 1918
[b] Mather and Jinks 1917

Fisher's (1918) parameters are related to m, the mean of the homozygotes whereas both Hayman (1958) and Kempthorne (1955, 1957) related their parameters to the mean of the F_2 population obtained by selfing from A_1A_2. Kempthorne's formulation estimates a negative value for dominance where there is positive heterosis. To overcome this difficulty it is suggested that when using this formulation the sign of the elements in the last column be changed. The same relationships between the specifications as given in Eqs. 33 and 34 will hold in the polygenic case.

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