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Transfer systems and covariance under assortative mating

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Summary. This paper introduces the concept of a transfer system of random variables and uses it ot study various types of assortative mating. The standard correlation structure between relatives under phenotypic and genetic assortative mating are obtained easily and these results are then extended to multiple characters by means of multivariate transfer systems. Equilibrium values for the parameters are found and index assortative mating is considered with specific applications.

Key words: Transfer systems – Assortative mating

|1| Introduction

The ideas of assortative mating for quantitative characters were introduced by Fisher (1918) in his classical and extremely difficult paper. The main results of this work are widely quoted (see Crow and Kimura 1970).

However, in an effort to find more comprehensible derivations, various authors have re-examined the topic from a number of viewpoints (Nagylaki 1978, 1982; Bulmer 1980) where further references may be found. One purpose of this paper is to introduce the idea of a transfer system of random variables and to show how it applies to assortative mating. Neglecting non-additive genetic effects, the standard results are quickly obtained and compared with those in the literature.

The main thrust of this work, though, is to use general transfer systems of vector random variables to allow the effects of assortative mating on several characters to be studied. From the practical point of view such an extension is required if, for instance, the effect of assortative mating on one variable on the rest is to be examined, see [7].

The phenotypic covariance matrices between various relatives are derived and the generalisations have a strong resemblance to their univariate counterparts. Both phenotypic and genetic assortative mating are considered and the relationship between the equilibrium and panmectic genetic covariance matrices is found.

In general terms a transfer system, as used in this application, is an ordered set of vector random variables such that the covariance between any two variables conditional on any third variable, which lies between the two in the ordering, is null. To the author's knowledge, such structures do not appear to have been used in the study of assortative mating. The main property of these systems is elementary and it will be developed in the subsequent sections.

|2| Statistical background and transfer systems

This section develops the idea of a transfer system of random variables and the concept is applied to assortative mating in subsequent sections. The treatment, for scalar random variables, pivots on properties of partial correlation analysis and this statistical tool will be briefly outlined. For further information see Kempthorne (1957, chapter 14).

Let X_1, X_2, X_3 be random variables. Without loss of generality it is assumed they have zero mean and unit variance. Let ϱ_{ij} be the regression of X_i on X_j and consider

$$X_{1.2} = X_1 - \varrho_{12} X_2, \quad X_{3.2} = X_3 - \varrho_{32} X_2 .$$

Thus, $X_{1.2}$, $X_{3.2}$ are the deviations of X_1 and X_3 from their best linear predictors using X_2.

The correlations between $X_{1.2}$ and $X_{3.2}$ is defined by

$$\varrho_{13.2} = C\,[X_{1.2},\ X_{3.2}]/\{V\,[X_{1.2}]\,V\,[X_{3.2}]\}^{1/2}$$
$$= (\varrho_{13} - \varrho_{12}\,\varrho_{32})/\{(1-\varrho_{12}^2)\,(1-\varrho_{32}^2)\}^{1/2} .$$

Necessarily, if $\varrho_{13.2} = 0$, $\varrho_{13} = \varrho_{12}\,\varrho_{32}$.

The interpretation of $\varrho_{13.2} = 0$ is that, apart from linear effects due to X_2 on X_1 and X_3, X_1 and X_3 are uncorrelated.

Consider now a system of $(n+1)$ random variables; $X_0, X_1, \ldots, X_n$ with $E[X_i] = \mu_i$ and $V[X_i] = \sigma_i^2$. If this system has the property that for all $i < j$ and for all $i < k < j$, $\varrho_{ij.k} = 0$, then it will be called a "transfer system".

It follows from the definition that

$$\varrho_{0n} = \prod_{i=0}^{n-1} \varrho_{i\,i+1} \tag{1}$$

since the result is certainly true for $n = 2$ and assuming it is true for $(n-1)$

$$\varrho_{0n.n-1} = 0 \Rightarrow \varrho_{0n} = \varrho_{0n-1}\,\varrho_{n-1n} = \prod_{i=0}^{n-1} \varrho_{i\,i+1}\,.$$

[3] Applications to assortative mating

To apply the above concept of a transfer system to assortative mating only requires clear diagrams, good notation and elementary genetic manipulations. Certain standard pedigrees will be considered and individuals labelled P_{ij}, where i refers to the number of generations previous to generation zero. Thus P_{ij} is the j^{th} individual in the pedigree at generation $-$ i.

The phenotypic and additive genetic values of P_{ij} will be written as p_{ij} and g_{ij}, each being expressed as a deviation from the population mean, and $V[p_{ij}] = \sigma_p^2(i)$, $V[g_{ij}] = \sigma_g^2(i)$.

Under random meating there is zero phenotypic and genetic correlation between mates. However, when some form of assortative mating is practiced this assumption is no longer valid.

Suppose P_{i0} and P_{i1} are mates then assortative mating introduces a correlation between g_{i0} and g_{i1} which will be referred to as m_g. The relationship which m_g bears to $\varrho[p_{i0}, p_{i1}] = m_p$ depends on the type of assortative mating which is practiced. In the case of phenotypic assortative mating, as will be shown, $m_g = h^2 m_p$ where $h^2 = \sigma_g^2/\sigma_p^2$, and under genetic assortative mating $m_p = h^2 m_g$.

These results can be established immediately by considering the appropriate transfer systems and using (1). Let $S_p = \{g_{i0}, p_{i0}, p_{i1}, g_{i1}\}$ and $S_g = \{p_{i0}, g_{i0}, g_{i1}, p_{i1}\}$ be transfer systems. Then, S_p and S_g are pertinent to phenotypic and genetic assortative mating respectively and $\varrho[g_{i0}, g_{i1}] = m_g = h\,m_p\,h = h^2 m_p$ while $\varrho[p_{i0}, p_{i1}] = m_p = h\,m_g\,h = h^2 m_g$, see [5].

The first pedigree considered will be that of n^{th}-order parent-child. For this and subsequent predigrees there will be a clear diagram and the derivations will be carried out under specific headings, firstly assuming phenotypic assortative mating. Notes will indicate the necessary changes if genetic assortative mating is used.

nth order parent-child

Required: $\varrho[p_{n0}, p_{00}]$

Transfer system: $\{p_{n0}, g_{n-10}, g_{n-20}, \ldots, g_{00}, p_{00}\}$

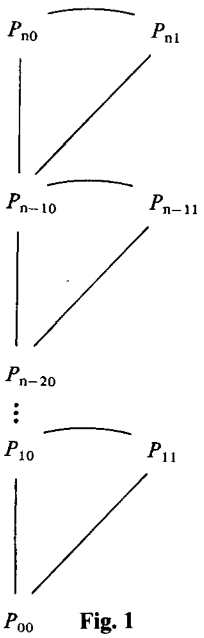

Fig. 1

Ingredients:

(i) $\varrho[p_{n0}, g_{n-10}] = \varrho[p_{n0}, \tfrac{1}{2}(g_{n0} + g_{n1})]$
$= \tfrac{1}{2}\varrho[p_{n0}, g_{n0}] + \tfrac{1}{2}\varrho[p_{n0}, g_{n1}]$
$= \dfrac{h}{2}(1 + m_p)$ (using S_p)

(ii) $\varrho[g_{i0}, g_{i-10}] = \varrho[g_{i0}, \tfrac{1}{2}(g_{i0} + g_{i1})] = \tfrac{1}{2}(1 + m_g)$

(iii) $\varrho[g_{00}, p_{00}] = h$

Result: $\varrho[p_{n0}, p_{00}] = \dfrac{h^2}{2}(1 + m_p)\left[\dfrac{1 + m_g}{2}\right]^{n-1}$.

Note. If genotypic assortative mating is practiced S_g must be referred to in (i) instead of S_p and hence $\dfrac{h}{2}(1 + m_p)$ becomes $\dfrac{h}{2}(1 + m_g)$ so that

$$\varrho[p_{n0}, p_{00}] = h^2\left[\frac{1 + m_g}{2}\right]^n.$$

Full-sibs

Required: $\varrho[p_{00}, p_{01}]$

Transfer system: $\{p_{00}, g_{00}, g_{01}, p_{01}\}$

Ingredients:

(i) $\varrho[p_{00}, g_{00}] = \varrho[g_{01}, p_{01}] = h$

(ii) $\varrho[g_{00}, g_{01}] = \varrho[\tfrac{1}{2}(g_{10} + g_{11}), \tfrac{1}{2}(g_{10} + g_{11})]$
$= \tfrac{1}{2}(1 + m_g)$

Result: $\varrho[p_{00}, p_{01}] = \dfrac{h^2}{2}(1 + m_g)$.

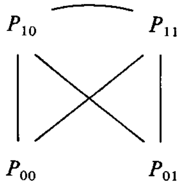

Fig. 2

Half-sibs

Required: $\varrho[p_{00}, p_{01}]$

Transfer system: $\{p_{00}, g_{00}, g_{01}, p_{01}\}$

Ingredients:

(i) $\varrho[p_{00}, g_{00}] = \varrho[g_{01}, p_{01}] = h$

(ii) $\varrho[g_{00}, g_{01}] = \varrho[\frac{1}{2}(g_{10} + g_{11}), \frac{1}{2}(g_{11} + g_{12})]$
$= \frac{1}{4}(1 + 2m_g + \varrho[g_{10}, g_{12}])$.

The transfer system connecting g_{10} and g_{12} is $\{g_{10}, p_{10}, p_{11}, p_{12}, g_{12}\}$, by the system of mating, hence

$\varrho[g_{10}, g_{12}] = h\, m_p\, m_p\, h = h^2 m_p^2 = m_p m_g$ and

$\varrho[g_{00}, g_{01}] = \frac{1}{4}[1 + m_g(2 + m_p)]$.

Result: $\varrho[p_{00}, p_{01}] = \dfrac{h^2}{4}[1 + m_g(2 + m_p)]$.

Note. If genotypic assortative mating is practiced the transfer system of (ii) is $\{p_{10}, g_{10}, g_{11}, g_{12}, p_{12}\}$ and $\varrho[g_{10}, g_{12}] = m_g^2$ so that

$$\varrho[p_{00}, p_{01}] = h^2\left[\frac{1 + m_g}{2}\right]^2.$$

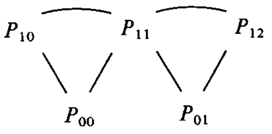

Fig. 3

Uncle-nephew

Required: $\varrho[p_{00}, p_{12}]$

Transfer system: $\{p_{00}, g_{00}, g_{11}, g_{12}, p_{12}\}$

Ingredients:

(i) $\varrho[p_{00}, g_{00}] = \varrho[g_{12}, p_{12}] = h$

(ii) $\varrho[g_{00}, g_{11}] = [\frac{1}{2}(g_{10} + g_{11}), g_{11}] = \frac{1}{2}(1 + m_g)$

(iii) $\varrho[g_{11}, g_{12}] = \frac{1}{2}(1 + m_g)$ (from full-sib).

Result: $\varrho[p_{00}, p_{12}] = h^2\left[\dfrac{1 + m_g}{2}\right]^2$.

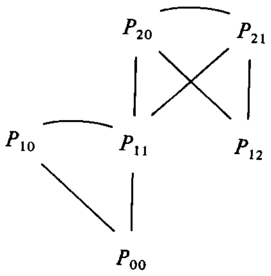

Fig. 4

Single first cousins

Required: $\varrho[p_{00}, p_{01}]$

Transfer system: $\{p_{00}, g_{00}, g_{11}, g_{12}, g_{01}, p_{01}\}$

Ingredients:

(i) $\varrho[p_{00}, g_{00}] = \varrho[g_{01}, p_{01}] = h$

(ii) $\varrho[g_{00}, g_{11}] = \varrho[g_{12}, g_{01}] = (1 + m_g)/2$

(iii) $\varrho[g_{11}, g_{12}] = (1 + m_g)/2$.

Result: $\varrho[p_{00}, p_{01}] = h^2\left[\dfrac{1 + m_g}{2}\right]^3$.

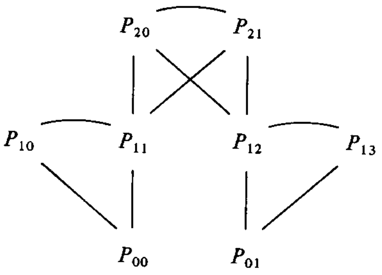

Fig. 5

Double first cousins

Required: $\varrho[p_{00}, p_{01}]$

Transfer systems:

basic: $\{p_{00}, g_{00}, g_{01}, p_{01}\}$

auxiliary: $\{g_{00}, g_{10}, g_{11}, g_{01}\}$; $\{g_{00}, g_{10}, g_{12}, g_{13}, g_{01}\}$
$\{g_{00}, g_{12}, g_{13}, g_{01}\}$; $\{g_{00}, g_{12}, g_{13}, g_{11}, g_{01}\}$

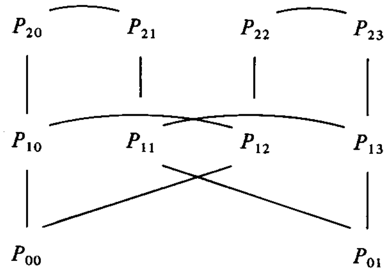

Fig. 6

Ingredients:

(i) $\varrho[p_{00}, g_{00}] = \varrho[g_{01}, p_{01}] = h$

(ii) $\varrho[g_{00}, g_{01}] = \varrho[\tfrac{1}{2}(g_{10}+g_{12}), \tfrac{1}{2}(g_{11}+g_{13})]$
$= \tfrac{1}{4}\{\varrho[g_{10}, g_{11}] + \varrho[g_{10}, g_{13}] + \varrho[g_{12}, g_{11}]$
$+ \varrho[g_{12}, g_{13}]\}$.

Using the auxiliary transfer systems

$$\varrho[g_{10}, g_{11}] = \varrho[g_{12}, g_{13}] = (1+m_g)/2 \quad \text{(from full-sibs)}$$

$$\varrho[g_{10}, g_{13}] = \varrho[g_{12}, g_{11}] = m_g(1+m_g)/2$$

so that

$$\varrho[g_{00}, g_{01}] = \tfrac{1}{2}[(1+m_g)/2 + m_g(1+m_g)/2] = \left[\frac{1+m_g}{2}\right]^2$$

Result: $\varrho[p_{00}, p_{01}] = h^2 \left[\frac{1+m_g}{2}\right]^2$.

The above results are summarised in Table 1. The first column of formulae lists the expressions for the correlation coefficients under phenotypic assortative mating which dictates m_p and induces $m_g = h^2 m_p$. The adjacent column gives the necessary changes if the assortative mating is genetic and hence specifies m_g and induces $m_p = h^2 m_g$.

The result for half-sibs agrees with that of Nagylaki (1978) but disagrees with Bulmer (1980). On the other hand, the correlation between double first-cousins in this table agrees with Bulmer (1980) but disagrees with Fisher's result (Crow and Kimura 1970).

Table 1

Relationship	Correlation	
	Phenotypic assortative mating ($m_g = h^2 m_p$)	Genotypic assortative mating ($m_p = h^2 m_g$)
n^{th} order parent-child	$\frac{h^2}{2}(1+m_p)\left[\frac{1+m_g}{2}\right]^{n-1}$	$h^2\left[\frac{1+m_g}{2}\right]^{n}$
Full-sibs	$h^2\left[\frac{1+m_g}{2}\right]$	
Half-sibs	$\frac{h^2}{4}[1+m_g(2+m_p)]$	$h^2\left[\frac{1+m_g}{2}\right]^{2}$
Uncle-nephew	$h^2\left[\frac{1+m_g}{2}\right]^{2}$	
Single first-cousin	$h^2\left[\frac{1+m_g}{2}\right]^{3}$	
Double first-cousin	$h^2\left[\frac{1+m_g}{2}\right]^{2}$	

[4] Multivariate transfer systems

In order to extend the results of assortative mating to several characters, it is necessary to introduce transfer systems for vector random variables. The work is technically a little more involved but the additional effort is well spent.

Let $\{X_0, X_1, \ldots, X_n\} = S$ be a set of random vectors of dimensions $k_0, k_1, \ldots, k_n$. Suppose that $E[X_i] = 0$, $V[X_i] = V_{ii}(k_i \times k_i)$ and $C[X_i X_j] = V_{ij}(k_i \times k_j]$. Consider any three variables X_i, X_j, X_k where $i < j < k$ and suppose that the conditional variables $X_i | X_j$ and $X_k | X_j$ can be represented by

$$X_i | X_j = V_{ij} V_{jj}^{-1} X_j + \varepsilon_{ij}$$

$$X_k | X_j = V_{kj} V_{jj}^{-1} X_j + \varepsilon_{kj}$$

where $E[\varepsilon_{ij}] = 0$, $E[\varepsilon_{kj}] = 0$, $C[\varepsilon_{ij}, \varepsilon_{kj}] = C[X_i X_j | X_j] = 0$, $V[\varepsilon_{ij}] = V_{ii} - V_{ij} V_{jj}^{-1} V_{ji}$ and $V[\varepsilon_{kj}] = V_{kk} - V_{kj} V_{jj}^{-1} V_{jk}$. A system satisfying the above conditions will be called a transfer system and, for such systems

$$C[X_i, X_k] = V_{ij} V_{jj}^{-1} V_{jk}.$$

The term $V_{ij} V_{jj}^{-1} X_j$ is, in a sense, the best linear predictor of X_i given X_j and, under the conditions, it is the conditional expectation of X_i given X_j. Similarly for X_k. Thus, in a transfer system the association between X_i and X_k is explained entirely by the linear association of these variables with X_j. Notice that if *S* is a multivariate normal system, the conditions for a transfer system can certainly be realised.

Anyway,

$$V_{0n} = V_{01} V_{11}^{-1} V_{12} V_{22}^{-1} V_{23} \ldots V_{n-1\,n-1}^{-1} V_{n-1\,n}, \quad n \geqq 2 \qquad (2)$$

since it is true for n = 2 and assuming that it holds for n − 1

$$V_{0n} = V_{0n-1} V_{n-1\,n-1}^{-1} V_{n-1\,n}.$$

The result (1) of section [2] follows from (2) as a special case.

[5] Applications to assortative mating

In order to discuss multi-character assortative mating it is necessary to set up the appropriate structure. Assume there are k characters with phenotypic and genetic vectors p and g, all measurements being taken from the population mean vector. Put

$$C[p, p] = P, \; C[g, g] = C[g, p] = G$$

and consider phenotypic and genetic assortative mating involving the vectors p and g. In fact, let P_{i0} and P_{i1} be mates at generation i with phenotypes and genotypes (p_{i0}, g_{i0}) and (p_{i1}, g_{i1}). Then under assortative mating

$$C[g_{i0}, g_{i1}] = C_g(i), \; C[p_{i0}, p_{i1}] = C_p(i)$$

and since this type of mating should be characterised by the correlation structure $C_p(i) = \Delta_p(i) M_p \Delta_p(i)$ and

$C_g(i) = \Delta_g(i)\; M_g \Delta_g(i)$ where

$\Delta_p(i) = \mathrm{diag}(\sqrt{P_{11}(i)}, \ldots, \sqrt{P_{kk}(i)})$,

$\Delta_g(i) = \mathrm{diag}(\sqrt{G_{11}(i)}, \ldots, \sqrt{G_{kk}(i)})$

and M_p, M_g are the respective correlation matrices induced by the scheme of mating.

In any case, to establish the relationship between C_p and C_g the two sets of vectors

$S_p = \{g_{i0}, p_{i0}, p_{i1}, g_{i1}\}$ and $S_g = \{p_{i0}, g_{i0}, g_{i1}, p_{i1}\}$

are required as transfer systems. In fact, applying (2) and S_p for phenotypic assortative mating $C_g(i) = C[g_{i0}, g_{i1}] = G(i)\,P(i)^{-1}\,C_p(i)\,P(i)^{-1}\,G(i)$. For genotypic assortative mating use S_g and (2) to show that $C_p(i) = G(i)\,G(i)^{-1}\,C_g(i)\,G(i)^{-1}\,G(i) = C_g(i)$ and $C_g(i)$ and $C_p(i)$ are the counterparts of $h^2 m_g$ and $h^2 m_p$ for the single character case.

It is clear that the multicharacter treatment of assortative mating is considerably more complicated to the univariate case. The same format as was adopted earlier will be followed here, reference being made to the appropriate figures.

n^{th} order parent-child (Fig. 1)

Transfer system: $\{p_{n0}, g_{n-10}, g_{n-20}, \ldots, g_{00}, p_{00}\}$.

Required: $C[p_{n0}, p_{00}]$

Ingredients:

(i) $C[p_{n0}, g_{n-10}] = C[p_{n0}, \tfrac{1}{2}(g_{n0} + g_{n1})]$

$$= \tfrac{1}{2}G + \tfrac{1}{2}C[p_{n0}, g_{n1}]$$

$$= \tfrac{1}{2}G + \tfrac{1}{2}C_p P^{-1} G \quad (\text{from } S_p)$$

$$= \left[\frac{I + C_p P^{-1}}{2}\right] G = G\left[\frac{I + P^{-1} C_p}{2}\right]$$

(ii) $C[g_{i0}, g_{i-10}] = C[g_{i0}, \tfrac{1}{2}(g_{i0} + g_{i1})] = \tfrac{1}{2}G + \tfrac{1}{2}C_g$

$$= G\left[\frac{I + G^{-1} C_g}{2}\right]$$

(iii) $C[g_{00}, p_{00}] = G$

Result: $G\left[\frac{I + P^{-1} C_p}{2}\right] \cdot G^{-1} \cdot G\left[\frac{I + G^{-1} C_g}{2}\right] \ldots G^{-1} G$

$$= G\left[\frac{I + P^{-1} C_p}{2}\right]\left[\frac{I + G^{-1} C_g}{2}\right]^{n-1}.$$

Note. If genotypic assortative mating is used S_g must be referred to in (i) and in this case

$C[p_{n0}, g_{n-10}] = \tfrac{1}{2}[C[p_{n0}, g_{n0}] + C[p_{n0}, g_{n1}]]$

$$= \tfrac{1}{2}[G + GG^{-1}C_g] = G\left[\frac{I + G^{-1} C_g}{2}\right]$$

and

$$C[p_{n0}, p_{00}] = G\left[\frac{I + G^{-1} C_g}{2}\right]^n.$$

Full sibs (Fig. 2)

Required: $C[p_{00}, p_{01}]$

Transfer system: $\{p_{00}, g_{00}, g_{01}, p_{01}\}$

Ingredients:

(i) $C[p_{00}, g_{00}] = C[g_{01}, p_{01}] = G$

(ii) $C[g_{00}, g_{01}] = C[\tfrac{1}{2}(g_{10} + g_{11}), \tfrac{1}{2}(g_{10} + g_{11})]$

$$= G\left[\frac{I + G^{-1} C_g}{2}\right]$$

Result: $C[p_{00}, p_{01}] = GG^{-1}G\left[\frac{I + G^{-1} C_g}{2}\right] G^{-1} G$

$$= G\left[\frac{I + G^{-1} C_g}{2}\right].$$

Half sibs (Fig. 3)

Required: $C[p_{00}, p_{01}]$

Transfer system:

basic: $\{p_{00}, g_{00}, g_{01}, p_{01}\}$;

auxiliary: $\{g_{10}, p_{10}, p_{11}, p_{12}, g_{12}\}$.

Ingredients:

(i) $C[p_{00}, g_{00}] = C[g_{01}, p_{01}] = G$

(ii) $C[g_{00}, g_{01}] = C[\tfrac{1}{2}(g_{10} + g_{11}), \tfrac{1}{2}(g_{11} + g_{12})]$

$$= \tfrac{1}{4}[G + 2C_g + C[g_{10}, g_{12}]].$$

Using the auxiliary transfer system which is specific to phenotypic assortative mating

$C[g_{10}, g_{12}] = GP^{-1}C_pP^{-1}C_pP^{-1}G$ and

Result:

$$C[p_{00}, p_{01}] = \frac{G}{4}[I + 2G^{-1}C_g + P^{-1}C_pP^{-1}C_pP^{-1}G].$$

Note. If genotypic assortative mating is used the required auxiliary transfer system is $\{p_{10}, g_{10}, g_{11}, g_{12}, p_{12}\}$ and $C[g_{10}, g_{12}] = C_g G^{-1} C_g$ so that

$$C[p_{00}, p_{01}] = \tfrac{1}{4}[G + 2C_g + C_g G^{-1} C_g] = G\left[\frac{I + G^{-1} C_g}{2}\right]^2$$

Uncle-nephew (Fig. 4)

Required: $C[p_{00}, p_{12}]$

Transfer system: $\{p_{00}, g_{00}, g_{11}, g_{12}, p_{12}\}$

Ingredients:

(i) $C[p_{00}, g_{00}] = C[g_{12}, p_{12}] = G$

(ii) $C[g_{00}, g_{11}] = C[\tfrac{1}{2}(g_{10} + g_{11}), g_{11}] = G\left[\frac{I+G^{-1}C_g}{2}\right]$

(iii) $C[g_{11}, g_{12}] = G\left[\frac{I+G^{-1}C_g}{2}\right]$ (from full-sibs)

$$\text{Result: } GG^{-1}G\left[\frac{I+G^{-1}C_g}{2}\right]G^{-1}G\left[\frac{I+G^{-1}C_g}{2}\right]G^{-1}G$$

$$= G\left[\frac{I+G^{-1}C_g}{2}\right]^2.$$

Single first cousins (Fig. 5)

Required: $C[p_{00}, p_{01}]$

Transfer system: $\{p_{00}, g_{00}, g_{11}, g_{12}, g_{01}, p_{01}\}$

Ingredients:

(i) $C[p_{00}, g_{00}] = C[g_{12}, p_{12}] = G$

(ii) $C[g_{00}, g_{11}] = C[\tfrac{1}{2}(g_{10} + g_{11}), g_{11}],$

$$= G\left[\frac{I+G^{-1}C_g}{2}\right] = C[g_{12}, g_{01}]$$

(iii) $C[g_{11}, g_{12}] = G\left[\frac{I+G^{-1}C_g}{2}\right]$ (from full-sibs)

$$\text{Result: } C[p_{00}, p_{01}] = GG^{-1}G\left[\frac{I+G^{-1}C_g}{2}\right]$$

$$G^{-1}G\left[\frac{I+G^{-1}C_g}{2}\right]G^{-1}G\left[\frac{I+G^{-1}C_g}{2}\right]G^{-1}G$$

$$= G\left[\frac{I+G^{-1}C_g}{2}\right]^3.$$

Double first cousins (Fig. 6)

Required: $C[p_{00}, p_{01}]$

Transfer systems:

basic: $\{p_{00}, g_{00}, g_{01}, p_{01}\}$,

auxiliary: $\{g_{00}, g_{10}, g_{11}, g_{01}\}, \{g_{00}, g_{10}, g_{12}, g_{13}, g_{01}\}$

$\{g_{00}, g_{12}, g_{13}, g_{01}\}, \{g_{00}, g_{12}, g_{13}, g_{11}, g_{01}\}$

Ingredients:

(i) $C[p_{00}, g_{00}] = C[g_{01}, p_{01}] = G$

(ii) $C[g_{00}, g_{01}] = C[\tfrac{1}{2}(g_{10} + g_{12}), \tfrac{1}{2}(g_{11} + g_{13})]$

$$= \tfrac{1}{4}\,[C[g_{10}, g_{11}] + C[g_{10}, g_{13}]$$
$$+ C[g_{12}, g_{11}] + C[g_{12}, g_{13}]].$$

Using the auxiliary transfer system

$$C[g_{10}, g_{11}] = C[g_{12}, g_{13}] = G\left[\frac{I+G^{-1}C_g}{2}\right]$$

(from full-sibs)

$$C[g_{10}, g_{13}] = C[g_{12}, g_{11}] = C[g_{10}, g_{12}]G^{-1}C[g_{12}, g_{13}]$$

$$= C_g G^{-1} G\left[\frac{I+G^{-1}C_g}{2}\right] = C_g\left[\frac{I+G^{-1}C_g}{2}\right]$$

and

$$C[g_{00}, g_{01}] = G\left[\frac{I+G^{-1}C_g}{2}\right]^2.$$

$$\text{Result: } C[p_{00}, p_{01}] = GG^{-1}G\left[\frac{I+G^{-1}C_g}{2}\right]^2 G^{-1}G$$

$$= G\left[\frac{I+G^{-1}C_g}{2}\right]^2.$$

The above results are summarised in Table 2 which is the analogue of Table 1. The same comments apply to the second and third columns.

[6] Parameters at equilibrium

For a single character with additive genetic variance σ_g^2 under panmixia, it has long been known that the equilibrium variance under assortative mating is $\hat{\sigma}_g^2 = \sigma_g^2/(1 - m_g)$. This has been established in a variety of ways; in particular a simple model for assortative mating proposed by Wright (1921) and lucidly discussed by Crow and Kimura (1970) leads to this result as the number of determining loci increase without limit.

However, Bulmer (1980) has used the following argument, which yields the required results very simply. Let P_{00} be an individual in the current generation with parents P_{10} and P_{11}. Then a model for g_{00} is

$$g_{00} = E[g_{00} \mid g_{10}, g_{11}] + \varepsilon = \tfrac{1}{2}(g_{10} + g_{11}) + \varepsilon.$$

This model holds irrespective of the mating system so that, for instance, under panmixia

$$\sigma_g^2 = V[\tfrac{1}{2}(g_{10} + g_{11})] + V[\varepsilon] \Rightarrow V[\varepsilon] = \sigma_g^2/2.$$

Thus, under assortative mating one is lead immediately to the recurrence relation

$$\sigma_g^2(n) = \sigma_g^2(n-1)(1 + m_g)/2 + \sigma_g^2/2$$

showing that in particular

$$\sigma_g^2(1) = \sigma_g^2(1 + m_g/2) \quad \text{and} \quad \hat{\sigma}_g^2 = \sigma_g^2/(1 - m_g).$$

when m_g is invariant.

Table 2

Relationship	Covariance matrices	
	Phenotypic assortative mating $(C_g = G P^{-1} C_p P^{-1} G)$	Genotypic assortative mating $(C_p = C_g)$
nth order parent-child	$G\left[\frac{I + P^{-1} C_p}{2}\right]\left[\frac{I + G^{-1} C_g}{2}\right]^{n-1}$	$G\left[\frac{I + G^{-1} C_g}{2}\right]^{n}$
Full-sibs	$G\left[\frac{I + G^{-1} C_g}{2}\right]$	
Half-sibs	$\frac{G}{4}[I + 2G^{-1} C_g + P^{-1} C_p P^{-1} C_p P^{-1} G]$	$G\left[\frac{I + G^{-1} C_g}{2}\right]^{2}$
Uncle-nephew	$G\left[\frac{I + G^{-1} C_g}{2}\right]^{2}$	
Single first cousins	$G\left[\frac{I + G^{-1} C_g}{2}\right]^{3}$	
Double first cousins	$G\left[\frac{I + G^{-1} C_g}{2}\right]^{2}$	

On the other hand, if m_p is the invariant, $m_g(n) = h^2(n)\, m_p$, where

$$h^2(n) = \sigma_g^2(n)/(\sigma_g^2(n) + \sigma_e^2),\ \sigma_g^2 + \sigma_e^2 = \sigma_p^2,$$

n refers to the n^{th} generation after the start of assortative mating and $\sigma_g^2 = \sigma_g^2(0)$. Using $\hat{}$ to denote equilibrium values

$$\hat{\sigma}_g^2 = \sigma_g^2/(1 - \hat{h}^2 m_p), \quad \hat{h}^2 = \hat{\sigma}_g^2/(\hat{\sigma}_g^2 + \sigma_e^2)$$

and these expressions can be used to define $\hat{h}^2$ in terms of σ_g^2, σ_e^2 and m_p, Bulmer (1980).

In general write

$$g_{00} = E[g_{00} \mid g_{01}, g_{11}] = \tfrac{1}{2}(g_{01} + g_{11}) + \varepsilon$$

where $E[\varepsilon] = 0$. Since the model holds for panmictic populations in particular, $V[\varepsilon] = G/2$. At generation n

$$G(n) = \tfrac{1}{2}[G(n-1) + C_g(n-1)] + G/2$$

which gives

$$G(1) = G[I + G^{-1} C_g/2], \quad \hat{G} - \hat{C}_g = G.$$

If the mating is such that

$$C_g(n) = C_g = G(n) P^{-1}(n) C_p(n) P^{-1}(n) G(n)$$

is invariant, a situation which is achieved by choosing $C_p(n) = P^{-1}(n) G(n) C_g G(n) P^{-1}(n)$, the equilibrium equation becomes

$$\hat{G} = C_g + G.$$

Otherwise, with $C_p(n) = \Delta_p(n) M_p \Delta_p(n)$, M_p invariant, the equation must be solved iteratively using the equations for $G(n)$ and $C_g(n)$.

On the other hand, writing $C_g(n) = \Delta_g(n) M_g(n) \Delta_g(n)$ and if $M_g(n) \equiv M_g$ is invariant, then as an extension of the single character case, let $\hat{G} = \hat{\Delta}_g \hat{R}_g \hat{\Delta}_g$, $\hat{\Delta}_g = \mathrm{diag}(\hat{G}_{11}, \ldots, \hat{G}_{kk})$, then

$$\hat{\Delta}_g \hat{R}_g \hat{\Delta}_g - \hat{\Delta}_g M_g \hat{\Delta}_g = G.$$

This implies that $\hat{G}_{ii} = G_{ii}/(1 - m_{gii})$ and that

$$\hat{G} = G + \hat{\Delta}_g M_g \hat{\Delta}_g.$$

It can be shown that the same result follows by an extension of Wright's model for assortative mating.

[7] Index assortative mating

It may be that individuals are mated on the basis of some index $I(p) = p'\beta$ or $I(g) = g'\beta$ where β is a set of weights which may be arrived at in a variety of ways. For instance, the usual weights for the phenotypic selection index is $\beta = P^{-1} Ga$, where a is a vector of economic weights. This form of mating requires certain changes to be made to the results of [6] and these are outlined briefly here.

Firstly, the mating transfer systems must be converted to

$$S_{I(p)} = \{g_{i0}, p_{i0}, I_{i0}(p), I_{i1}(p), p_{i1}, g_{i1}\}$$

$$S_{I(g)} = \{p_{i0}, g_{i0}, I_{i0}(g), I_{i1}(g), g_{i1}, p_{i1}\}.$$

It is now possible to calculate the C_p and C_g matrices required for [5]. In fact

$$C_g = G\beta\beta' G\, m_{I(p)}/(\beta' P \beta), \ C_p = P\beta\beta' P\, m_{I(p)}/\beta' P \beta;$$

$$C_p = G\beta\beta' G\, m_{I(g)}/(\beta' G \beta), C_g = G\beta\beta' G\, m_{I(g)}/\beta' G \beta;$$

where $m_{I(p)}$ and $m_{I(g)}$ are phenotypic and the genetic correlations between the indexes of mates.

It is noted that under phenotypic assortative mating $m_{I(g)} = h^2_{I(p)} m_{I(p)}$ and under genotypic assortative mating $m_{I(p)} = h^2_{I(p)} m_{I(g)}$, where $h^2_{I(p)}$ is the heritability of $p'\beta$.

Further alterations are needed to the results for half-sibs; in particular the auxiliary set becomes, under phenotypic assortative mating,

$$\{g_{10}, p_{10}, I_{10}(p), I_{11}(p), I_{12}(p), p_{12}, g_{11}\}$$

which gives

$$C[g_{10}, g_{12}] = m_{I(p)} C_g .$$

Under genetic assortative mating this transfer system becomes

$$\{p_{10}, g_{10}, I_{10}(g), I_{11}(g), I_{12}(g), g_{12}, p_{12}\}$$

and

$$C[g_{10}, g_{12}] = m_{I(g)} C_p .$$

No further adjustments appear necessary.

It is the form of the mating transfer set which specifies the system of mating. Thus, $I_{I(p)}$ and $I_{I(g)}$ can be specialised to investigate the effect of assortative mating on one character on the rest by putting the appropriate element of β equal to unity and the rest zero. In this case C_g and C_p take special forms which can be substituted into the expressions of [5].

Some explicit results have been derived by Gianola (1982) and it is instructive to verify some of the equilibrium formulae reported in that paper. It is noted firstly that, restricting attention to two characters and practicing phenotypic assortative mating on the first character only, $\beta' = (1, 0)$,

$$C_g(n) = G(n)\beta\beta' G(n)\, m_1/P_{11}(n)$$

where $\beta\beta' = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}$, and m_1 is the phenotypic correlation between the first character for the two mates. This can be written as

$$C_g(n) = \Delta_g(n)\, M_g(n)\, \Delta_g(n),$$
$$\Delta_g^2(n) = \mathrm{diag}(G_{11}(n), G_{22}(n))$$

where

$$M_g(n) = m_1 h_1^2(n) \begin{bmatrix} 1 & \varrho_g(n) \\ \varrho_g(n) & \varrho_g^2(n) \end{bmatrix}$$

and $h_1^2(n)$, is the heritability for the first character at generation n and $\varrho_g(n)$ the genetic correlation between the two characters. It is assumed that m_1 is invariant and characteristic of the mating system.

Letting $\hat{}$ indicate equilibrium values, from Section [6]

$$\hat{\Delta}_g \hat{R}_g \hat{\Delta}_g - \hat{\Delta}_g \hat{M}_g \hat{\Delta}_g = \hat{\Delta}_g \hat{N}_g \hat{\Delta}_g = G$$

where

$$\hat{N}_g = \begin{bmatrix} 1 - \hat{h}_1^2 m_1 & \hat{\varrho}_g(1 - \hat{h}_1^2 m_1) \\ \hat{\varrho}_g(1 - \hat{h}_1^2 m_1) & 1 - \hat{h}_1^2 m_1 \hat{\varrho}_g^2 \end{bmatrix}.$$

This establishes that

$$\hat{G}_{11}(1 - \hat{h}_1^2 m_1) = G_{11}, \quad \hat{G}_{22}(1 - \hat{h}_1^2 m_1 \hat{\varrho}_g^2) = G_{22},$$
$$\sqrt{\hat{G}_{11}}\sqrt{\hat{G}_{22}}\, \hat{\varrho}_g(1 - \hat{h}_1^2 m_1) = G_{12}$$

from which it follows that

$$\hat{\varrho}_g = \varrho_g / \sqrt{1 - \hat{h}_1^2 m_1 (1 - \varrho_g^2)}$$

after some algebra. These results are identical to (7), (8) and (12) of Gianola (1982); this paper should be consulted for further explicit results and discussions of application.

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