Assortative Mating and the Genetic Correlation

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Summary. The effect of assortative mating on the genetic correlation between traits X and Y is considered. Assortation on trait X changes the magnitude of the genetic correlation but not its sign. There are two situations depending on the signs of the correlation between mates (ϱ) and of the random mating genetic correlation (θ): 1) if sign (θ) = sign (ϱ), then $\hat{\theta} > \theta$, where $\hat{\theta}$ is the genetic correlation at equilibrium after continued assortation, and 2) if sign (θ) $\neq$ sign (ϱ), then $\hat{\theta} < \theta$. However, negative assortative mating is virtually powerless to alter the magnitude of the genetic correlation. The consequences of a "mixed" assortation model, e.g., high milk production females mated to fast growing males and lesser productive females mated to slower growing sires, were also studied. "Mixed" positive assortation always increases the genetic correlation, but negative assortation decreases it. The implications of assortative mating on correlated responses to selection and on the equilibrium covariances between relatives for pairs of traits are discussed.

Key words: Assortative mating – Genetic correlation – Covariance between relatives – Correlated responses

Introduction

When the individuals in a mating pair are phenotypically more similar or dissimilar than what they would otherwise be if the pairs were chosen at random from a population, it is said that the mating is assortative. If the phenotypic value of both mates deviates from the mean of the population in the same direction, mating is positive assortative; if the deviation of one of the mates is positive and the other is negative, mating is negative assortative.

Jennings (1916) and Wentworth and Remick (1916) studied the consequences of assortative mating for a single locus, two alleles, model. Assortative mating under polygenic inheritance was considered by Fisher (1918), Wright (1921),

Crow and Felsenstein (1968), Bulmer (1980) and several other authors. In a multifactorial model, assortative mating has limited impact on heterozygosity unless the correlation between the phenotypes of mates is nearly unity and the number of loci is small (Lush 1948; Crow and Felsenstein 1968). Also, positive assortative mating substantially increases the genetic variance, particularly if the trait is highly heritable (e.g. Bulmer 1980). The approach to equilibrium, both in terms of heterozygosity and genetic variance, is rapid, with most of the increase in variance occurring in the first two generations after assortation starts. Reeve (1953, 1961) considered the estimation of the genetic correlation from offspring-parent covariances when parents were mated assortatively. Latter (1965) derived the covariance between half-sibs and the effects of genotype × environment interaction on the covariance between traits of *Phalaris tuberosa* under assortative mating.

Several artificial breeding companies in the USA offer "corrective mating programs". These consist of choosing a bull mate on the basis of the attributes of individual cows. "Corrective" mating involves negative assortation, i.e., mating bulls that excel in some trait in which the cows are deficient. Dishman et al. (1981) presented data suggesting that negative assortative mating is widely practiced in the US dairy industry. It is, therefore, important to take into account the effect of assortative mating on estimation of genetic parameters and sire evaluation programs. Otherwise, estimates of heritabilities and genetic correlations would be biased, and the prediction error variance of sire evaluation by progeny test would be unnecessarily large.

This paper describes the effect of assortative mating on the genetic correlation between traits and the equilibrium covariance between full-sibs, half-sibs, offspring-parent and grandoffspring-grandparents for pairs of traits. These covariances are those usually employed to estimate genetic parameters in animal breeding applications. The expressions for the equilibrium covariances would permit taking into account assortative mating in genetic evaluation models.

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Conventional Assortation Model

Assortative mating is practiced for a trait X and the correlation between mates is ϱ. The models describing

the relationship between the additive genotypic values of an offspring (A_X^O, A_Y^O; Y is another trait) and those of his parents (A_X^S, A_Y^S, A_X^D, A_Y^D) are

$$A_X^O = \tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X,\tag{1}$$

$$A_Y^O = \tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e_Y,\tag{2}$$

where $e_X \sim (O, \text{Var}_A^X/2)$ and $e_Y \sim (O, \text{Var}_A^Y/2)$ are random segregation residuals with $\text{Cov}(e_X, e_Y) = \text{Cov}_A^{XY}/2$, where Cov_A^{XY} is the additive genetic covariance under random mating. Equations (1) and (2) permit to write the recursive relationship

$$\text{Cov}_{A(t+1)}^{XY} = \tfrac{1}{2}\,\text{Cov}_{A(t)}^{XY} + \tfrac{1}{4}\,\text{Cov}(A_X^S, A_Y^D)$$
$$+ \tfrac{1}{4}\,\text{Cov}(A_X^D, A_Y^S) + \tfrac{1}{2}\,\text{Cov}_A^{XY},\tag{3}$$

where $\text{Cov}_{A(t)}^{XY}$ is the additive genetic covariance at time t. Under multivariate normality, one can consider the conditional expectations of the genotypic values given the X-values (Bulmer 1980) and write

$$\text{Cov}(A_X^S, A_Y^D) = \text{Cov}[h_{X(t)}^2 (X^S - \mu_X), \theta_{(t)}\, h_{X(t)}\, h_{Y(t)}$$
$$\cdot\, \sigma_{X(t)}^{-1}\, \sigma_{Y(t)} (X^D - \mu_X)]$$
$$= \text{Cov}_{A(t)}^{XY}\, \varrho\, h_{X(t)}^2 = \text{Cov}(A_X^D, A_Y^S),\tag{4}$$

where $h_{X(t)}^2$ and $h_{Y(t)}^2$ are the heritabilities of X and Y, respectively, at time t; $\sigma_{X(t)}^2$ and $\sigma_{Y(t)}^2$ are phenotypic variances at time t, $\theta_{(t)}$ is the genetic correlation at time t, and $\mu_X = E(X^S) = E(X^D)$. Hence, (3) becomes

$$\text{Cov}_{A(t+1)}^{XY} = \tfrac{1}{2}\,\text{Cov}_{A(t)}^{XY}(1 + \varrho\, h_{X(t)}^2) + \tfrac{1}{2}\,\text{Cov}_A^{XY}.\tag{5}$$

At equilibrium, $\text{Cov}_{A(t+1)}^{XY} = \text{Cov}_{A(t)}^{XY} = \hat{\text{Cov}}_A^{XY}$, and rearranging (5), one obtains

$$\hat{\theta} = \frac{\theta}{1 - h_X^2\, \varrho} \left(\frac{\text{Var}_A^X\, \text{Var}_A^Y}{\hat{\text{Var}}_A^X\, \hat{\text{Var}}_A^Y}\right)^{1/2}\tag{6}$$

where $\hat{\theta}$ and θ are the equilibrium and random mating genetic correlations, $\hat{h}_X^2$ is the equilibrium heritability of X, and $\hat{\text{Var}}_A^X$, $\hat{V}_A^Y$ are the equilibrium additive genetic variances of X and Y, respectively.

The steady-state equations for the genetic variances of X and Y can be obtained in a similar manner with

$$\frac{V_A^X}{\hat{V}_A^X} = 1 - \varrho\, \hat{h}_X^2.\tag{7}$$

and

$$\frac{V_A^Y}{\hat{V}_A^Y} = 1 - \varrho\, \hat{h}_X^2\, \hat{\theta}^2.\tag{8}$$

Equation (7) illustrates the well known result (Crow and Felsenstein 1968) that positive assortative mating ($\varrho > 0$) increases the genetic variance: as ϱ and $\hat{h}_X^2$ increase, so does the ratio $\hat{V}_A^X/V_A^X$. Note from (8) that positive assortative mating also increases the genetic variance of a correlated trait (Y) to an extent depend-

ing on the magnitude of $\hat{\theta}$. The equilibrium heritabilities can be obtained by taking the total variances of X and Y in a random mating population as 1. Then $\hat{h}_X^2 = \hat{\text{Var}}_A^X/(\hat{\text{Var}}_A^X + 1 - h_X^2)$ can be used in (7) with $V_A^X = h_X^2$ to solve a quadratic equation on $\hat{V}_A^X$ (Bulmer 1980). Its positive root is

$$\hat{\text{Var}}_A^X = \frac{2h_X^2 - 1 + [1 - 4\varrho\, h_X^2(1 - h_X^2)]^{1/2}}{2(1 - \varrho)}.\tag{9}$$

Likewise, the equilibrium genetic variance of the correlated trait Y would be

$$\hat{\text{Var}}_A^Y = \frac{2h_Y^2 - 1 + [1 - 4\varrho\, \theta^2\, h_X^2(1 - h_X^2)]^{1/2}}{2(1 - \varrho\,\theta^2)}\tag{10}$$

and $\hat{h}_Y^2 = \hat{\text{Var}}_A^Y/(\hat{\text{Var}}_A^Y + 1 - h_Y^2)$. Note that (10) depends on $\hat{\theta}$, the equilibrium genetic correlation.

Using (7) and (8) Eq. (6) can be written as

$$\hat{\theta} = \theta \left(\frac{1 - \varrho\, \hat{h}_X^2\, \hat{\theta}^2}{1 - \varrho\, \hat{h}_X^2}\right)^{1/2}\tag{11}$$

which indicates that assortation for X changes the magnitude of the genetic correlation between X and Y but cannot change its sign. Equation (11) can be solved explicitly for $\hat{\theta}$ as

$$\hat{\theta} = \theta \sqrt{\frac{1}{1 - \varrho\, \hat{h}_X^2(1 - \theta^2)}},\tag{12}$$

yielding the following conditions:

1) If $\theta > 0$ and $\varrho > 0$, then $\hat{\theta} > \theta$;
2) If $\theta > 0$ and $\varrho < 0$, then $\hat{\theta} < \theta$;
3) If $\theta < 0$ and $\varrho > 0$, then $\hat{\theta} < \theta$; and
4) If $\theta < 0$ and $\varrho < 0$, then $\hat{\theta} > \theta$.

Values of $\hat{\theta}$ for selected combinations of θ, ϱ and h_X^2 are presented in Table 1. Negative assortative mating is virtually powerless to alter the magnitude of the genetic correlation, even when the absolute value of the random mating genetic correlation is large or when the trait for which assortation is practiced (X) is highly heritable. On the other hand, strong positive assortative mating can have a marked effect on the genetic correlation, particularly if the heritability of X is large. This could be useful in animal improvement programs. In swine, for example, backfat thickness and amount of lean in the carcass are negatively genetically correlated, i.e., selection against high backfat results in leaner carcass. Positive assortative mating for backfat would increase the genetic variance of backfat thickness and of amount of lean, and would make the genetic correlation between the two more strongly negative. Hence, selection against backfat with positive assortative mating of parents would be expected to yield a larger correlated response in lean cuts than if assortation were not practiced. The expected correlated re-

Table 1. Values of the equilibrium genetic correlation under assortative mating for trait X for selected combinations of the random mating genetic correlation (θ), the correlation between mates (ϱ) and the heritability of X (h_X^2)

| θ | ϱ | h_X^2 |
		0.05	0.20	0.40	0.60
− 0.6	− 1.0	− 0.59	− 0.57	− 0.54	− 0.52
	0.4	− 0.60	− 0.62	− 0.64	− 0.66
	0.8	− 0.61	− 0.64	− 0.71	− 0.78
− 0.4	− 1.0	− 0.39	− 0.37	− 0.35	− 0.34
	0.4	− 0.40	− 0.42	− 0.43	− 0.45
	0.8	− 0.41	− 0.44	− 0.50	− 0.59
− 0.2	− 1.0	− 0.20	− 0.19	− 0.17	− 0.16
	0.4	− 0.20	− 0.21	− 0.22	− 0.23
	0.8	− 0.20	− 0.22	− 0.26	− 0.32
0.2	− 1.0	0.20	0.19	0.17	0.16
	0.4	0.20	0.21	0.22	0.23
	0.8	0.20	0.22	0.26	0.32
0.4	− 1.0	0.39	0.37	0.35	0.34
	0.4	0.40	0.42	0.43	0.45
	0.8	0.41	0.44	0.50	0.59
0.6	− 1.0	0.59	0.57	0.54	0.52
	0.4	0.60	0.62	0.64	0.66
	0.8	0.61	0.64	0.71	0.78

sponse of a trait Y to selection for a trait X under assortative mating can be expressed relative to the expected correlated response under random mating of parents as

$$\frac{\Delta G_{Y.X} \text{ (Assortative)}}{\Delta G_{Y.X} \text{ (Random)}} = \frac{\theta}{\theta} \left(\frac{\hat{V}ar_A^Y}{Var_A^Y} \right)^{1/2} \frac{\tilde{h}_X}{h_X}$$

$$= \frac{\tilde{h}_X}{h_X} \left\{ \frac{1}{[1 - \varrho\,\tilde{h}_X^2(1 - \theta^2)](1 - \varrho\,\tilde{h}_X^2\,\theta^2)} \right\}^{1/2}. \quad (13)$$

In the case of backfat (X) and amount of lean (Y) we can take $h_X^2 = .50$, and $\theta = -.80$ (Jensen et al. 1967). Assuming $\varrho = .80$, one obtains $\tilde{h}_X^2 = .691$, and $\tilde{\theta} = -.89$. Hence, (13) becomes

$$\Delta G_{Y.X}(\text{Assortative})/\Delta G_{Y.X}(\text{Random}) = 1.75,$$

i.e., the correlated response in amount of lean in the carcass can be increased by about 75% by positively assorting parents on the basis of their backfat thickness measurements. Likewise, if two traits have a positive, favorable genetic correlation such as milk yield and protein yield per lactation, positive assortative mating of parents for milk yield in a selection program for this trait would enhance the correlated response in protein yield. If X and Y have a positive or negative unfavorable genetic correlation such as growth rate and calving difficulty or milk yield and fat test, negative assortative

mating of parents would reduce the absolute value of the genetic correlation to a limited extent (Table 1) but would decrease the genetic variance (Eqs. 7, 8).

Positive assortation on X would increase the genetic variance of Y more than direct assortation on Y if

$$\frac{V_A^Y}{\hat{V}_A^Y} < \frac{V_A^Y}{\tilde{V}_A^Y}, \quad (14)$$

where $\tilde{V}_A^Y$ is the equilibrium genetic variance of Y when positive assortation is for Y. Assuming that the marital correlation is the same under both systems, the inequality in (14) can be written as

$$1 - \varrho\,\tilde{h}_X^2\,\theta^2 < 1 - \varrho\,\tilde{h}_Y^2, \quad (15)$$

where $\tilde{h}_Y^2$ is the equilibrium heritability of Y under direct assortation for Y. Equivalently, (14) implies

$$\tilde{h}_Y^2/\tilde{h}_X^2 < \theta^2 \quad (16)$$

indicating, in general, that positive assortation for a highly correlated trait of high heritability (X) would be more effective in increasing the genetic variance of Y than positive assortation on Y itself. For example, suppose birth weight (X) and "health status" at weaning (Y) in sheep have parameters $h_X^2 = .25$, $h_Y^2 = .05$ and $\theta = .40$ in a random mating population. If parents are positively assorted on their birth weights with $\varrho = .8$, then $\tilde{h}_X^2 = .31$ and $\tilde{\theta} = .45$. On the other hand, if parents are assorted on their "health status" scores, $\tilde{h}_Y^2 = .052$ and $\tilde{\theta} = .41$. Since $.052/.31 < (.45)^2$, response to selection for "health"score would be larger if parents are assorted positively for birth weight than if they are assorted on "health" scores themselves. Positive assortation for "health" scores would yield a larger response than no assortation at all.

Mixed Assortation Model

Mating pairs are assorted such that the correlation between the phenotypic values of traits X in the males, say, and Y in the females, is ϱ^*. This type of assortative mating arises when complementarity is to be obtained in the offspring, e.g., high milk production females are mated to fast growing males. It can also arise with sex limited traits: females of high ovulation rate mated to males of large scrotal circumference. The models describing the relationship between the additive genotypic values of an offspring and those of his parents are as in (1) and (2).

For the X-variate

$$Var_{A(t+1)}^X = \tfrac{1}{2} Var_{A(t)}^X + \tfrac{1}{2} Cov(A_X^S, A_X^D) + \tfrac{1}{2} Var_A^X. \quad (17)$$

Now, in the conditional distribution under multivariate normality, write

$$\text{Cov}(A_X^S, A_X^D) = \text{Cov}[h_{X(t)}^2 (X^S - \mu_X),$$

$$\cdot\, \theta_{(t)}\, h_{X(t)}\, h_{Y(t)}\, \sigma_{X(t)}\, \sigma_{Y(t)}^{-1}\, (Y^D - \mu_Y)]$$

$$= \theta_{(t)}\, h_{X(t)}\, h_{Y(t)}\, \varrho^*\, \text{Var}_{A(t)}^X\,. \tag{18}$$

Hence,

$$\text{Var}_{A(t+1)}^X = \tfrac{1}{2} \text{Var}_{A(t)}^X (1 + \theta_{(t)}\, h_{X(t)}\, h_{Y(t)}\, \varrho^*) + \tfrac{1}{2} \text{Var}_A^X \tag{19}$$

and, at equilibrium

$$\frac{\text{Var}_A^X}{\hat{\text{Var}}_A^X} = 1 - \hat\theta\, \hat{h}_X\, \hat{h}_Y\, \varrho^*. \tag{20}$$

If sign $(\hat\theta) = \text{sign}(\varrho^*)$, then $\hat{\text{Var}}_A^X > \text{Var}_A^X$; otherwise, $\text{Var}_A^X > \hat{\text{Var}}_A^X$.

Similarly,

$$\text{Var}_{A(t+1)}^Y = \tfrac{1}{2}\text{Var}_{A(t)}^Y (1 + \theta_{(t)}\, h_{X(t)}\, h_{Y(t)}\, \varrho^*) + \tfrac{1}{2}\text{Var}_A^Y, \tag{21}$$

with the steady-state equation being

$$\frac{\text{Var}_A^Y}{\hat{\text{Var}}_A^Y} = 1 - \hat\theta\, \hat{h}_X\, \hat{h}_Y\, \varrho^*. \tag{22}$$

A comparison of (20) and (21) indicates that this mixed assortation model elicits the same relative change in the genetic variances of X and Y.

The recursive relationship for the additive genetic covariance is

$$\text{Cov}_{A(t+1)}^{XY} = \tfrac{1}{2}\, \text{Cov}_{A(t)}^{XY}$$
$$+ \tfrac{1}{4}\, [\text{Cov}(A_X^S, A_Y^D) + \text{Cov}(A_X^D, A_Y^S)]$$
$$+ \tfrac{1}{2}\, \text{Cov}_A^{XY}. \tag{23}$$

In the conditional distribution of the multivariate normal model

$$\text{Cov}(A_X^S, A_Y^D) = \text{Cov}[h_{X(t)}^2 (X^S - \mu_X), h_{Y(t)}^2 (Y^D - \mu_Y)]$$

$$= h_{X(t)}^2\, h_{Y(t)}^2\, \varrho^*\, \sigma_{X(t)}\, \sigma_{Y(t)}\,, \tag{24}$$

and

$$\text{Cov}(A_Y^S, A_X^D) = \theta_{(t)}^2\, h_{X(t)}^2\, h_{Y(t)}^2\, \varrho^*\, \sigma_{X(t)}\, \sigma_{Y(t)}. \tag{25}$$

Using (24) and (25) in Eq. (23) we can write, after some algebra

$$\text{Cov}_{A(t+1)}^{XY} = \tfrac{1}{2}\, \text{Cov}_{A(t)}^{XY} \left[1 + \tfrac{1}{2}\, \varrho^*\, h_{X(t)}\, h_{Y(t)} \left(\frac{\theta_{(t)}^2 + 1}{\theta_{(t)}} \right) \right]$$
$$+ \tfrac{1}{2}\, \text{Cov}_A^{XY}. \tag{26}$$

At equilibrium

$$\hat\theta (\hat{\text{Var}}_A^X\, \hat{\text{Var}}_A^Y)^{1/2} \left[1 - \tfrac{1}{2}\, \varrho^*\, \hat{h}_X\, \hat{h}_Y \left(\frac{\hat\theta^2 + 1}{\hat\theta} \right) \right]$$
$$= \theta (\text{Var}_A^X\, \text{Var}_A^Y)^{1/2}, \tag{27}$$

which, using (20) and (22), can be rewritten as

$$\hat\theta - \tfrac{1}{2}\, \hat{h}_X\, \hat{h}_Y\, \varrho^*(\hat\theta^2 + 1) = \theta(1 - \hat\theta\, \hat{h}_X\, \hat{h}_Y\, \varrho^*), \tag{28}$$

and note that $\hat\theta = \theta$ only if $\varrho^* = 0$. Letting $k = \hat{h}_X\, \hat{h}_Y\, \varrho^*$, (28) can be rearranged as a quadratic equation on $\hat\theta$

$$\left(\frac{k}{2} \right) \hat\theta^2 - (1 + \theta k)\, \hat\theta + \frac{k}{2} + \theta = 0, \tag{29}$$

which has two distinct real roots as

$$\Delta = (1 + \theta k)^2 - 4\frac{k}{2}\left(\frac{k}{2} + \theta \right)$$
$$= 1 + k^2(\theta^2 - 1)$$

is always positive. This is so because $\Delta > 0$ implies $\theta^2 > (k^2 - 1)/k^2$, which is always true because $|k| < 1$. The two roots of (29) are

$$\hat\theta = \theta + \frac{1}{k} \pm \sqrt{\theta^2 + \frac{1}{k^2} - 1}. \tag{30}$$

This expression is not explicit in $\hat\theta$ because k depends on $\hat{h}_X$ and $\hat{h}_Y$ which, in turn, depend on $\hat\theta$ (Eqs. 20, 22). However, we have the following cases:

1) Mixed Positive Assortation ($\varrho^* > 0$) Always Increases the Genetic Correlation

To prove this, consider the statement $\hat\theta < \theta$. From (30) this is equivalent to proving that $k^{-1} + (\theta^2 + k^{-2} - 1)^{1/2} < 0$, and $k^{-1} - (\theta^2 + k^{-2} - 1)^{1/2} < 0$. The first expression can never be true as with $\varrho^* > 0$, k^{-1} is positive, and $k^{-2} - 1$ is also positive. The second statement with $\varrho^* > 0$, would be equivalent to $\theta^2 > 1$, which can never be true. Hence, if $\varrho^* > 0$, $\hat\theta < \theta$ is false. Therefore, if $\varrho^* > 0$, the genetic correlation is always increased.

2) Mixed Negative Assortation ($\varrho^* < 0$) Always Decreases the Genetic Correlation

Consider $\hat\theta > \theta$. From (30) this would be equivalent to $k^{-1} + (\theta^2 + k^{-2} - 1)^{1/2} > 0$, and $k^{-1} - (\theta^2 + k^{-2} - 1)^{1/2} > 0$. The first expression can be written as

$$(\theta^2 + k^{-2} - 1)^{1/2} > -k^{-1}$$

implying $\theta^2 > 1$, which is never true. Likewise, the second statement implies $k^{-1} > (\theta^2 + k^{-2} - 1)^{1/2}$, which can never be true as with $\varrho^* < 0$, $k^{-1} < 0$. Hence, if $\varrho^* < 0$, the statement $\hat\theta > \theta$ is false and the genetic correlation is always reduced.

In summary, mixed positive assortation ($\varrho^* > 0$) would be indicated for traits with favorable positive genetic correlations, e.g., growth rate and amount of lean tissue in the carcass in beef cattle, or for traits with unfavourable negative genetic correlations such as milk yield and protein percentage. On the other hand, mixed negative assortation could be useful to reduce unfavorable positive genetic correlations (growth rate and feed intake) or to enhance negative favorable negative genetic correlations such as backfat thickness and feed efficiency. Equations (20) and (22) indicate, however, that positive mixed assortation will decrease

the additive genetic variance of the traits in question if the genetic correlation between them is negative. Similarly, negative mixed assortation will decrease the genetic variance if the genetic correlation is positive.

Covariances Between Relatives

Several authors (e.g., Fisher 1918; Bulmer 1980) derived the correlation between relatives for a trait under assortative mating. Reeve (1953, 1961) obtained offspring-parent covariances for pairs of traits, and Latter (1965) presented the correlation between half-sibs. In this section, we consider full-sibs, half-sibs, offspring-parent and grandoffspring-grandparent covariances as these are the ones usually utilized in animal breeding for estimation of genetic parameters. The basic assumptions involve a population in equilibrium after repeated assortative mating and those of Bulmer's (1980) infinitesimal model, i.e., that contributions of the dominance and environmental components to the covariance between relatives are unaffected by assortative mating. We present the additive genetic contribution to the covariances between relatives.

Full-sibs

The phenotypic values of sibs 1 and 2 are X^{o_1}, Y^{o_1}, X^{o_2} and Y^{o_2}, and let $E_X^{o_1}$, $E_Y^{o_1}$, $E_X^{o_2}$, $E_Y^{o_2}$ be environmental effects affecting sib records. Using (1)

$$\text{Cov}(X^{o_1}, X^{o_2})$$
$$= \text{Cov}(\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X + E_X^{o_1}, \tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e'_X + E_X^{o_2})$$
$$= \tfrac{1}{2} \hat{\text{Var}}_A^X + \tfrac{1}{2} \text{Cov}(A_X^S, A_X^D), \tag{31}$$

as the segregation residuals e_X and e'_X are independently distributed. The variables A_X^S, A_X^D can be replaced by their expectations conditional on the sire and dam's phenotypes so

$$\text{Cov}(A_X^S, A_X^D) = \text{Cov}[\hat{h}_X^2(X^S - \mu_X), \hat{h}_X^2(X^D - \mu_X)]$$
$$= \hat{h}_X^2 \varrho \, \hat{\text{Var}}_A^X. \tag{32}$$

Hence, (31) becomes

$$\text{Cov}(X^{o_1}, X^{o_2}) = \tfrac{1}{2} \hat{\text{Var}}_A^X (1 + \varrho \, \hat{h}_X^2). \tag{33}$$

Similarly,

$$\text{Cov}(X^{o_1}, Y^{o_2})$$
$$= \text{Cov}[\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X + E_X^{o_1}, \tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e'_Y + E_Y^{o_2}]$$
$$= \tfrac{1}{2} \hat{\text{Cov}}_A^{XY} + \tfrac{1}{4} [\text{Cov}(A_X^S, A_Y^D) + \text{Cov}(A_X^D, A_Y^S)]. \tag{34}$$

Replacing A_X^S, A_Y^D, A_X^D, A_Y^S by their conditional means

$$\text{Cov}[A_X^S, A_Y^D] = \text{Cov}[A_X^D, A_Y^S] = \hat{h}_X^2 \, \hat{\text{Cov}}_A^{XY} \varrho, \tag{35}$$

and using (35) in (34)

$$\text{Cov}(X^{o_1}, Y^{o_2}) = \tfrac{1}{2} \hat{\text{Cov}}_A^{XY}(1 + \varrho \, \hat{h}_X^2). \tag{36}$$

Also,

$$\text{Cov}(Y^{o_1}, Y^{o_2}) = \text{Cov}(\tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e_Y + E_Y^{o_1},$$
$$\cdot \tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e'_Y + E_Y^{o_2}) = \tfrac{1}{2} \hat{\text{Var}}_A^Y(1 + \theta^2 \, \hat{h}_X^2 \varrho). \tag{37}$$

Half-sibs

The notation is as before, with o_1 and o_2 denoting the half-sibs in question, and D_1 and D_2 indicating their unrelated dams. The following covariances are considered: $\text{Cov}(X^{o_1}, X^{o_2})$, $\text{Cov}(X^{o_1}, Y^{o_2}) = \text{Cov}(X^{o_2}, Y^{o_1})$, and $\text{Cov}(Y^{o_1}, Y^{o_2})$.

First

$$\text{Cov}(X^{o_1}, X^{o_2})$$
$$= \text{Cov}[\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^{D_1} + e_X + E_X^{o_1}, \tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^{D_2} + e'_X + E_X^{o_2}]. \tag{38}$$

Then

$$\text{Cov}(X^{o_1}, X^{o_2}) = \tfrac{1}{4} \hat{\text{Var}}_A^X + \tfrac{1}{4} [\text{Cov}(A_X^S, A_X^{D_2})$$
$$+ \text{Cov}(A_X^{D_1}, A_X^S) + \text{Cov}(A_X^{D_1}, A_X^{D_2})]. \tag{39}$$

In the conditional distribution, $E(A_X^S | X^S) = \hat{h}^2(X^S - \mu_X)$, and $E(A_X^{D_i} | X^S) = \hat{h}_X^2 \varrho(X^S - \mu_X)$, for $i = 1, 2$. Replacing random variables by their conditional expectations

$$\text{Cov}(X^{o_1}, X^{o_2}) = \tfrac{1}{4} \hat{\text{Var}}_A^X + \tfrac{1}{2} \hat{h}_X^2 \varrho \, \hat{\text{Var}}_A^X + \tfrac{1}{4} \hat{h}_X^2 \varrho^2 \, \hat{\text{Var}}_A^X$$
$$= \tfrac{1}{4} \hat{\text{Var}}_A^X [1 + \hat{h}_X^2 \varrho(2 + \varrho)]. \tag{40}$$

The contribution of the additive genetic variance is identical to the result obtained by Latter (1965) but differs from the one presented by Bulmer (1980).

The second covariance of interest is

$$\text{Cov}(X^{o_1}, Y^{o_2}) = \tfrac{1}{4} \hat{\text{Cov}}_A^{XY} [1 + \hat{h}_X^2 \varrho(2 + \varrho)]. \tag{41}$$

Finally,

$$\text{Cov}(Y^{o_1}, Y^{o_2}) = \tfrac{1}{4} \hat{\text{Var}}_A^Y [1 + \theta^2 \, \hat{h}_X^2 \varrho(2 + \varrho)]. \tag{42}$$

Offspring-Parent

The covariances of interest are $\text{Cov}(X^o, X^S)$, $\text{Cov}(X^o, Y^S)$ $\text{Cov}(Y^o, X^S)$ and $\text{Cov}(Y^o, Y^S)$; the superscripts o and S indicate offspring and sire, respectively. First, we have

$$\text{Cov}(X^o, X^S) = \text{Cov}(\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X + E_X^o, X^S)$$
$$= \tfrac{1}{2} \text{Cov}[\hat{h}_X^2 - \mu_X), X^S] + \tfrac{1}{2} \text{Cov}[\hat{h}_X^2(X^D - \mu_X), X^S]$$
$$= \tfrac{1}{2} \hat{\text{Var}}_A^X (1 + \varrho). \tag{43}$$

Similarly

$$\text{Cov}(X^o, Y^S) = \text{Cov}(\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X + E_X^o, Y^S)$$
$$= \tfrac{1}{2} \hat{\text{Cov}}_A^{XY} + \tfrac{1}{2} \text{Cov}[\hat{h}^2(X^D - \mu_X), \frac{\hat{\text{Cov}}_{XY}}{\hat{\text{Var}}_X}(X^S - \mu_X)]$$
$$= \tfrac{1}{2}(\hat{\text{Cov}}_A^{XY} + \hat{h}_X^2 \varrho \, \hat{\text{Cov}}_{XY}) \tag{44}$$

where $\hat{V}ar_X$ and $\hat{C}ov_{XY}$ are the equilibrium phenotypic variance and covariance, respectively. Also

$$\text{Cov}\,(Y^o, X^S) = \text{Cov}(\tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e_Y + E_Y^o, X^S)$$

$$= \tfrac{1}{2}\,\text{Cov}\left[\frac{\theta\,\hbar_X\,\hbar_Y\,\hat{\sigma}_X\,\hat{\sigma}_Y (X^S - \mu_X)}{\hat{\sigma}_X^2}, X^S\right]$$

$$+ \tfrac{1}{2}\,\text{Cov}\left[\frac{\theta\,\hbar_X\,\hbar_Y\,\hat{\sigma}_X\,\hat{\sigma}_Y (X^D - \mu_X)}{\hat{\sigma}_X^2}, X^S\right]$$

$$= \tfrac{1}{2}\,\hat{C}ov_A^{XY}(1 + \varrho). \tag{45}$$

The fourth covariance of interest is

$$\text{Cov}\,(Y^o, Y^S) = \text{Cov}[\tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e_Y + E_Y^o, Y^S]$$

$$= \tfrac{1}{2}\,\hat{V}ar_A^Y + \tfrac{1}{2}\,\text{Cov}\left[\frac{\theta\,\hbar_X\,\hbar_Y\,\hat{\sigma}_X\,\hat{\sigma}_Y}{\hat{\sigma}_X^2}(X^D - \mu_X),\right.$$

$$\left. \frac{\theta\,\hbar_X\,\hbar_Y\,\hat{\sigma}_X\,\hat{\sigma}_Y}{\hat{\sigma}_X^2}(X^S - \mu_X)\right] \tag{46}$$

$$= \tfrac{1}{2}\,\hat{V}ar_A^Y(1 + \theta^2\,\varrho\,\hbar_X^2). \tag{47}$$

Grand-Offspring-Grand-Parent

The variables X^o and Y^o denote phenotypic values in the grandoffspring and X^N, Y^N refer to measurements in the grandparent. The covariances of interest are $\text{Cov}\,(X^o, X^N)$, $\text{Cov}\,(X^o, Y^N)$, $\text{Cov}\,(Y^o, X^N)$ and $\text{Cov}\,(Y^o, Y^N)$.

Consider first

$$\text{Cov}(X^o, X^N) = \text{Cov}(\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X + E_X^o, X^N)$$

$$= \tfrac{1}{2}\,[\text{Cov}(A_X^S, X^N) + \text{Cov}(A_X^D, X^N)]. \tag{48}$$

Now

$$\text{Cov}\,(A_X^S, X^N) = \text{Cov}(\tfrac{1}{2} A_X^N + \tfrac{1}{2} A_X^{\tilde{N}} + e_X', X^N)$$

$$= \tfrac{1}{2}\,\{\text{Cov}\,[\hbar_X^2(X^N - \mu_X), X^N]$$

$$+ \text{Cov}\,[\hbar_X^2(X^{\tilde{N}} - \mu_X), X^N]\}$$

$$= \tfrac{1}{2}\,\hat{V}ar_A^X(1 + \varrho) \tag{49}$$

where $\tilde{N}$ is the other parent of S. Furthermore,

$$\text{Cov}(A_X^D, X^N) = \text{Cov}[\varrho\,\hbar_X^2(X^S - \mu_X), X^N]$$

$$= \tfrac{1}{2}\,\hat{V}ar_A^X(1 + \varrho)\,\varrho\,\hbar_X^2, \tag{50}$$

which follows from (43). Using (49) and (50) in (48)

$$\text{Cov}(X^o, X^N) = \tfrac{1}{4}\,\hat{V}ar_A^X(1 + \varrho)\,(1 + \varrho\,\hbar_X^2). \tag{51}$$

The second function of interest is

$$\text{Cov}(X^o, Y^N) = \text{Cov}(\tfrac{1}{2} A_X^S + \tfrac{1}{2} A_X^D + e_X + E_X^o, Y^N). \tag{52}$$

Replacing the A's by their expectations conditional on the X values, it can be shown that

$$\text{Cov}(A_X^S, Y^N) = \tfrac{1}{2}\,\hat{\sigma}_X\,\hat{\sigma}_Y(\theta\,\hbar_X\,\hbar_Y + r\,\varrho\,\hbar_X^2) \tag{53}$$

where r is the phenotypic correlation between X and Y. Likewise

$$\text{Cov}\,(A_X^D, Y^N) = \hbar_X^2\,\varrho\,\text{Cov}(X^S, Y^N) \tag{54}$$

$$= \tfrac{1}{2}\,\hbar_X^2\,\varrho(\theta\,\hbar_X\,\hbar_Y\,\hat{\sigma}_X\,\hat{\sigma}_Y + \hbar_X^2\,\varrho\,r\,\hat{\sigma}_X\,\hat{\sigma}_Y)$$

following from (44). Using (53) and (54) in (52)

$$\text{Cov}(X^o, Y^N) = \tfrac{1}{4}\,\hat{\sigma}_X\,\hat{\sigma}_Y(\theta\,\hbar_X\,\hbar_Y + r\,\varrho\,\hbar_X^2)\,(1 + \varrho\,\hbar_X^2). \tag{55}$$

The third covariance is

$$\text{Cov}(Y^o, X^N) = \text{Cov}(\tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e_Y + E_Y^o, X^N). \tag{56}$$

It can be shown that

$$\text{Cov}(A_Y^S, X^N) = \tfrac{1}{2}\,\hat{C}ov_A^{XY}(1 + \varrho) \tag{57}$$

and

$$\text{Cov}\,(A_Y^D, X^N) = \tfrac{1}{2}\,\hat{C}ov_A^{XY}\,\varrho\,\hbar_X^2(1 + \varrho). \tag{58}$$

Hence, (56) becomes

$$\text{Cov}\,(Y^o, X^N) = \tfrac{1}{2}\,\hat{C}ov_A^{XY}(1 + \varrho)\,(1 + \varrho\,\hbar_X^2). \tag{59}$$

Finally,

$$\text{Cov}\,(Y^o, Y^N) = \text{Cov}\,(\tfrac{1}{2} A_Y^S + \tfrac{1}{2} A_Y^D + e_Y + E_Y^o, Y^N). \tag{60}$$

Now

$$\text{Cov}\,(A_Y^S, Y^N) = \tfrac{1}{2}\,\hat{\sigma}_Y^2\,(\hbar_Y^2 + \theta\,\hbar_X\,\hbar_Y\,r\,\varrho). \tag{61}$$

Likewise

$$\text{Cov}\,(A_Y^D, Y^N) = \tfrac{1}{2}\,\hat{\sigma}_Y^2\,\hbar_X^2\,\varrho(\hbar_Y^2\,\theta^2 + \theta\,\hbar_X\,\hbar_Y\,r\,\varrho). \tag{62}$$

Collecting (61) and (62) in (60) one obtains

$$\text{Cov}\,(Y^o, Y^N)$$

$$= \tfrac{1}{4}\,\hat{\sigma}_Y^2\,[\hbar_Y^2\,(1 + \theta^2\,\hbar_X^2\,\varrho) + \theta\,\hbar_X\,\hbar_Y\,r\,\varrho(1 + \hbar_X^2\,\varrho)] \tag{63}$$

which yields the usual result for the grandoffspring-grandparent covariance under random mating by letting $\varrho = 0$.

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