

Genotype by environment interactions and genetic correlations involving two environmental factors*

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Summary. The concept of the genetic correlation for one trait across environments was extended to two environmental factors B and C. Three additive genetic correlations for the same trait were defined: r_G , across both environmental factors; $r_{G(B)}$, across C and within B; and $r_{G(C)}$, across B and within C. As genotype \times environment variances increase, the genetic correlations across environments decrease. These three genetic correlations are biased downward in the presence of heterogeneity of genetic variances within environments when they are calculated from the usual analysis of variance (r_G^* , $r_{G(B)}^*$, $r_{G(C)}^*$). Correction factors were derived to remove the bias. The two-way genotype by environment interaction variances can be biased upward or downward by the heterogeneity, but the three-way interaction variance is always biased upward. Correction factors for the interaction variances were also derived. Four additive genetic correlations between two traits (X and Y) were derived: $r_{G_{xy}}$, across both B and C; $r_{G(B)_{xy}}$ and $r_{G(C)_{xy}}$, across one environmental factor and within the other; and $r_{G(BC)_{xy}}$, within both B and C. These concepts were extended to genetic correlations for dominance and maternal effects. Paternal half-sib and factorial mating designs were used to obtain the various genetic correlations. An example of a paternal half-sib design with beef cattle was used to illustrate the methodology.

Key words: Genotype by environment Interaction – Genetic correlation – Cattle

Introduction

The concept of genotype by environment interaction may be stated very simply. If a particular genotype is superior in one environment but fails to be superior in a second environment, then genotype by environment interaction is said to be present. Falconer (1952) formalized this idea in terms of a genetic correlation by assuming that a character measured in two environments represents two distinct traits. On this basis the genetic correlation between the trait measured in the two environments indicates whether or not genotype by environment interaction is present. A genetic correlation of very nearly one implies that genotype by environment variance is negligible. In contrast, a genetic correlation that is less than one means that genotype by environment variance may be biologically important.

The genotype \times environment variance component can be partitioned into two parts, one associated with the genetic correlation and one associated with heterogeneity of genetic variances measured in each environment (Robertson 1959; Dickerson 1962; Yamada 1962; Eisen et al. 1963). Correcting for heterogeneity of variances provides unbiased genetic correlations for use in predicting correlated response to selection in one environment or for index selection in two or more environments. Heterogeneity does not affect the ranking of individuals in the various environments. In this sense, the genotype \times environment interaction variance component from the analysis of variance is biased upward by the heterogeneity of variances. This causes the genetic correlation to be biased downward when calculated as an intraclass correlation. Robertson (1959) first showed how to correct for this bias for the case of one environmental factor. Dickerson (1962) presented a detailed discussion of the application of

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these concepts to animal breeding strategies. Other approaches to interpreting the importance of genotype \times environment interactions have been given by Freeman (1973), Moav et al. (1975), Wright (1976) and Moll et al. (1978).

One objective of the present paper is to extend the interpretation of genotype \times environment interaction and the genetic correlation between a quantitative character measured at two or more levels of a single environmental factor to the case of two environmental factors, including the necessary adjustments for heterogeneity of genetic variances. The first section of the theory develops the genetic model. Following this, we discuss application of the theory to a typical paternal half-sib experiment. While only additive direct genetic effects have been considered for the most part in the literature on genotype \times environment interaction, other interactions may be present. Maternal genetic effects are known to play a significant role in growth traits of mammals (Cundiff 1972) and dominance effects may exist for fitness traits associated with life histories of species (Rose and Charlesworth 1981; Dingle and Hegmann 1982). Therefore, the third section of theory adapts a factorial experiment to estimate genotype \times environment variances which include both maternal and dominance genetic effects. The fourth section develops a natural extension of the theory to the genetic correlation between two traits measured in the same or in different environments, as suggested by Krause et al. (1965). An example from a subset of a beef cattle experiment is then used to illustrate the theory.

Theory

Genetic model

The model presented by Willham (1963) to account for direct and maternal autosomal diploid effects was extended to include genotype \times environment interactions. The assumptions are that individuals are sampled randomly from a random mating population that is in linkage and Hardy-Weinberg equilibrium.

Let P_{xwkl} represent the phenotypic value of individual x with dam w measured in the k th level of environmental factor B and l th level of environmental factor C . The model is

$$P_{xwkl} = A_x + D_x + A_{m_w} + D_{m_w} + E_{m_w} + B_k + C_l + (AB)_{xk} + (DB)_{xk} + (A_m B)_{wk} + (D_m B)_{wk} + (E_m B)_{wk} + (AC)_{xl} + (DC)_{xl} + (A_m C)_{wl} + (D_m C)_{wl} + (E_m C)_{wl} + (ABC)_{xkl} + (DBC)_{xkl} + (A_m BC)_{wkl} + (D_m BC)_{wkl} + (E_m BC)_{wkl} + (BC)_{kl} + E_{xwkl}$$

where A_x and D_x are additive direct and dominance direct effects of individual x ; A_{m_w} , D_{m_w} and E_{m_w} are

additive maternal, dominance maternal and maternal environmental effects of individual w ; B_k and C_l are the k th and l th level of the respective environmental factors; $(AB)_{xk}, \dots, (D_m BC)_{wkl}$ are respective genotype \times environment interactions; $(E_m B)_{wk}, \dots, (BC)_{kl}$ are environment \times environment interactions; and E_{xwkl} is a specific environmental deviation for individual x . The respective causal variance (V) and covariance (C) components are defined as $V_A, V_D, V_{A_m}, V_{D_m}, C_{AA_m}, C_{DD_m}, V_{E_m}, V_B, V_C, V_{AB}, V_{DB}, V_{A_m B}, V_{D_m B}, V_{E_m B}, C_{(AB)(A_m B)}, C_{(DB)(D_m B)}, V_{AC}, V_{DC}, V_{A_m C}, V_{D_m C}, V_{E_m C}, C_{(AC)(A_m C)}, C_{(DC)(D_m C)}, V_{ABC}, V_{DBC}, V_{A_m BC}, V_{D_m BC}, C_{(ABC)(A_m BC)}, C_{(DBC)(D_m BC)}, V_{E_m BC}, V_{BC}$ and V_E . If we now choose a second individual y with dam z , the covariance between P_{xwkl} and $P_{yzk'l'}$ will depend on the magnitude of these variances and covariances in addition to the relationship between x and y , w and z , x and z , and y and w , and whether the individuals are measured in the same or different environments. The possible covariances are summarized in Table 1. Two additional terms given in Table 1 must be defined. The coefficient of coancestry (r_{xy}, r_{wz}, r_{xz} and r_{yw}) is the probability that one gene at a locus in say x is identical by descent with one gene at that locus in say y . The coefficient u_{xy} is the probability that the two genes at a locus in x are identical by descent with the two genes at that locus in y , and similarly for u_{wz}, u_{xz} and u_{yw} .

From the covariances summarized in Table 1, it is clear that the covariance between individuals grown in the same environment include environment and genotype \times environment variances. On the other hand, the covariance between individuals reared in completely different environments is free of these variances. Cockerham (1963) and Comstock and Moll (1963) discussed these concepts but did not consider heterogeneity of genetic variances with multiple environmental classes.

Paternal half-sib design

A frequent method of estimating genetic parameters in nonlitter-bearing species is to mate randomly a sire to several dams where each mating produces one offspring (Becker 1975). In the present design, n progeny from each sire are allocated at random to each of the bc environmental subgroups. The assumptions are that the sires and dams are not inbred and are mutually unrelated. Relaxation of either of these assumptions can be incorporated into the analysis if necessary (Hinkelmann 1969, 1971; Van Vleck and Hudson 1981). The statistical model describing this design is

$$Y_{iklq} = \mu + s_i + b_k + c_l + (sb)_{ik} + (sc)_{il} + (bc)_{kl} + (sbc)_{ikl} + e_{iklq}$$

Table 1. Covariance among relatives when genotype by environment variances are present^b

Cov($P_{xwkl}, P_{yzk'l}$)	$2r_{xy}$	u_{xy}	$2r_{wz}$	u_{wz}
C_1 : x & y rel., $k = k', l = l'$,	$V_A + V_{AB} + V_{AC} + V_{ABC}$	$V_D + V_{DB} + V_{DC} + V_{DBC}$	$V_{A_m} + V_{A_mB} + V_{A_mC} + V_{A_mBC}$	$V_{D_m} + V_{D_mB} + V_{D_mC} + V_{D_mBC}$
C_2 : x & y rel., $k = k', l \neq l'$	$V_A + V_{AB}$	$V_D + V_{DB}$	$V_{A_m} + V_{A_mB}$	$V_{D_m} + V_{D_mB}$
C_3 : x & y rel., $k \neq k', l = l'$	$V_A + V_{AC}$	$V_D + V_{DC}$	$V_{A_m} + V_{A_mC}$	$V_{D_m} + V_{D_mC}$
C_4 : x & y rel., $k \neq k', l \neq l'$	V_A	V_D	V_{A_m}	V_{D_m}
C_5 to C_8 : x & y unrel.	0	0	0	0
	$2(r_{xz} + r_{yw})$	$u_{xz} + u_{zw}$		δ^a
C_1	$C_{AA_m} + C_{(AB)(A_mB)} + C_{(AC)(A_mC)} + C_{(ABC)(A_mBC)}$	$C_{DD_m} + C_{(DB)(D_mB)} + C_{(DC)(D_mC)} + C_{(DBC)(D_mBC)}$		$V_{E_m} + V_{E_mB} + V_{E_mC} + V_{E_mBC}$
C_2	$C_{AA_m} + C_{(AB)(A_mB)}$	$C_{DD_m} + C_{(DB)(D_mB)}$		$V_{E_m} + V_{E_mB}$
C_3	$C_{AA_m} + C_{(AC)(A_mC)}$	$C_{DD_m} + C_{(DC)(D_mC)}$		$V_{E_m} + V_{E_mC}$
C_4	C_{AA_m}	C_{DD_m}		V_{E_m}
C_5 to C_8	0	0		0
	β^a	γ^a	$\beta\gamma^a$	ε^a
C_1 & C_5 : $k = k', l = l'$	V_B	V_C	V_{BC}	V_E
C_2 & C_6 : $k = k', l \neq l'$	V_B	V_C	V_{BC}	V_E
C_3 & C_7 : $k \neq k', l = l'$	V_B	V_C	V_{BC}	V_E
C_4 & C_8 : $k \neq k', l \neq l'$	V_B	V_C	V_{BC}	V_E

^a $\delta = 1$ if $w = z$, $\delta = 0$ if $w \neq z$; $\beta = 1$ if $k = k'$, $\beta = 0$ if $k \neq k'$; $\gamma = 1$ if $l = l'$, $\gamma = 0$ if $l \neq l'$; $\varepsilon = 0$ if $x \neq y$, otherwise $\varepsilon = 1$

^b Column headings are coefficients of the variances and covariances in the body of the table

where Y_{iklq} is an observation of the trait in individual q born to sire i and measured in the k th level of environmental factor B and the l th level of environmental factor C ($i = 1, \dots, s$; $k = 1, \dots, b$; $l = 1, \dots, c$; $q = 1, \dots, n$), μ is the overall mean, s_i is a random sire effect, b_k and c_l are environmental effects, $(sb)_{ik}$, $(sc)_{il}$, $(bc)_{kl}$ and $(sbc)_{ikl}$ are respective interaction effects and e_{iklq} is a random error term. The effects of particular interest are the sire effect and the three interaction effects involving sires, and their definition depends on the assumption regarding the environmental factors B and C . If B and C are random then the respective variances are V_s , V_{sb} , V_{sc} and V_{sbc} ; if B and C are fixed then the variances are V'_s , V'_{sb} , V'_{sc} and V'_{sbc} ; if B is random and C fixed then the variances are V''_s , V''_{sb} , V''_{sc} and V''_{sbc} ; and if B is fixed and C random then the variances are V'''_s , V'''_{sb} , V'''_{sc} and V'''_{sbc} . In all cases e_{ijk} is NID with mean zero and variance V_e .

The expected mean squares based on each of the four assumptions are presented in Table 2. Observational components of variance are obtained by equating observed with expected mean squares and solving for the unknowns (Satterthwaite 1946). Approximate standard errors of the variance components can be found by applying the methods given by Searle (1971).

Expected mean squares for the three mixed models are based on an extension of the two-way mixed model given by Scheffé (1959) and labeled Model I by Hocking (1978). Hocking (1978) argued convincingly that definition of expected mean squares should be based on the biological meaning of the assumptions in the statistical model and presented his two-way mixed Model II which has expected mean squares essentially identical to the random model. This result can be used to explain how Yamada (1962) obtained the same estimate of genetic correlation for the same trait in different environments for both the mixed and random models. We argue, as implied by Yamada (1962), that the variance components with biological meaning are those estimated from the random model. Thus, further discussion will be based on observational variance components obtained from the random model. To obtain meaningful parameters from the mixed models, the following equivalences from Table 2 are used:

$$V_{sbc} = V'_{sbc} = V''_{sbc} = V'''_{sbc},$$

$$V_{sb} = V'_{sb} - \frac{1}{c} V'_{sbc} = V''_{sb} - \frac{1}{c} V''_{sbc} = V'''_{sb},$$

$$V_{sc} = V'_{sc} - \frac{1}{b} V'_{sbc} = V''_{sc} = V'''_{sc} - \frac{1}{b} V'''_{sbc},$$

Table 2. Analysis of variance and relevant expected mean squares for the paternal half-sib design with two environmental factors

Source	df	MS	Expected mean squares	
			Random model	B and C fixed
Env. B	$b - 1$	M_b		
Env. C	$c - 1$	M_c		
B \times C	$(b - 1)(c - 1)$	M_{bc}		
Sires (S)	$(s - 1)$	M_s	$V_e + nV_{sbc} + ncV_{sb} + nbV_{sc} + nbcV_s$	$V_e + nbcV'_s$
S \times B	$(s - 1)(b - 1)$	M_{sb}	$V_e + nV_{sbc} + ncV_{sb}$	$V_e + ncV'_{sb}$
S \times C	$(s - 1)(c - 1)$	M_{sc}	$V_e + nV_{sbc} + nbV_{sc}$	$V_e + nbV'_{sc}$
S \times B \times C	$(s - 1)(b - 1)(c - 1)$	M_{sbc}	$V_e + nV_{sbc}$	$V_e + nV'_{sbc}$
Error	$sbc(n - 1)$	M_e	V_e	V_e
			B random and C fixed	B fixed and C random
Env. B				
Env. C				
B \times C				
Sires (S)			$V_e + ncV''_{sb} + nbcV''_s$	$V_e + nbcV'''_{sc} + nbcV'''_s$
S \times B			$V_e + ncV''_{sb}$	$V_e + nV'''_{sbc} + ncV'''_{sb}$
S \times C			$V_e + nV''_{sbc} + nbV''_{sc}$	$V_e + nbV'''_{sc}$
S \times B \times C			$V_e + nV''_{sbc}$	$V_e + nV'''_{sbc}$
Error			V_e	V_e

$$V_s = V'_s - \frac{1}{b} V'_{sb} - \frac{1}{c} V'_{sc} + \frac{1}{bc} V'_{sbc}$$

$$= V''_s - \frac{1}{c} V''_{sc} = V'''_s - \frac{1}{b} V'''_{sb}$$

The genetic interpretation of the observational variance components can be derived by applying the covariances in Table 1 to the paternal half-sib experiment as follows:

$$C_1 = V_s + V_b + V_c + V_{bc} + V_{sb} + V_{sc} + V_{sbc}$$

$$= \frac{1}{4} (V_A + V_{AB} + V_{AC} + V_{ABC}) + V_B + V_C + V_{BC},$$

$$C_2 = V_s + V_b + V_{sb} = \frac{1}{4} (V_A + V_{AB}) + V_B,$$

$$C_3 = V_s + V_c + V_{sc} = \frac{1}{4} (V_A + V_{AC}) + V_C,$$

$$C_4 = V_s = \frac{1}{4} V_A,$$

and solving for the causal components gives

$$V_A = 4C_4 = 4V_s,$$

$$V_{AB} = 4(C_2 - C_4 - C_6) = 4V_{sb},$$

$$V_{AC} = 4(C_3 - C_4 - C_7) = 4V_{sc},$$

$$V_{ABC} = 4(C_1 - C_2 - C_3 - C_5 + C_4 + C_6 + C_7) = 4V_{sbc}.$$

The genetic correlation for the same trait averaged over both environmental classes B and C is

$$r_{G(C)}^* = V_A / (V_A + V_{AB} + V_{AC} + V_{ABC}). \quad (1)$$

In contrast, the genetic correlation for the same trait within environmental class B averaged over C is

$$r_{G(B)}^* = (V_A + V_{AB}) / (V_A + V_{AB} + V_{AC} + V_{ABC}) \quad (2)$$

and the genetic correlation within environmental class C averaged over B is

$$r_{G(C)}^* = (V_A + V_{AC}) / (V_A + V_{AB} + V_{AC} + V_{ABC}). \quad (3)$$

As for the case of one environmental factor, the numerators of these intraclass correlations are unbiased but the denominators are biased upward by heterogeneity of genetic variances among the environments. It will now be shown that the correction for heterogeneity is different for the three intraclass genetic correlations. This will be done by comparing the intraclass correlations to the interclass correlations, which are not affected by heterogeneity, obtained from analyses among and within environments.

Consider the four types of one-way analyses of variance and covariance among and within the environmental subclasses presented in Table 3. The covariance within sires across any environmental level has zero expectation since under the model the specific environmental errors for different individuals are uncorrelated. It is possible by chance for the data to be arranged in such a manner as to induce an apparent error covariance, C_e . In this case terms of the form

$$C_s + \frac{1}{n} C_e$$

should be used, i.e., the covariance among sire means. Following the development of Yamada (1962) we wish to put the sums of squares, or equivalently the mean squares, in the random model analysis of variance (Table 2) in terms of the components defined in Table 3. For example, the sum of squares

Table 3. One-way analyses of variance (ANOVA) within environmental subclasses and analyses of covariance (ANOCOVA) between environmental subclasses for the paternal half-sib design

Type of analysis	Source	df	Sum of squares (cross products)	EMS (CP)
ANOVA within B and C	Sires	$s - 1$	$\frac{1}{n} \sum_i Y_{ikl}^2 - \frac{1}{n s} Y_{.kl}^2$	$V_{ekl} + n V_{skl}$
	Error	$s(n - 1)$	$\sum_i \sum_q Y_{iklq}^2 - \frac{1}{n} \sum_i Y_{ikl}^2$	V_{ekl}
ANOCOVA across B within C ($k \neq k'$)	Sires	$s - 1$	$\frac{1}{n} \sum_i Y_{ikl} Y_{ik'l} - \frac{1}{n s} Y_{.kl} Y_{.k'l}$	$n C_{skk'l}$
	Error	$s(n - 1)$	—	—
ANOCOVA across C within B ($l \neq l'$)	Sires	$s - 1$	$\frac{1}{n} \sum_i Y_{ikl} Y_{ik'l} - \frac{1}{n s} Y_{.kl} Y_{.k'l}$	$n C_{skk'l'}$
	Error	$s(n - 1)$	—	—
ANOCOVA across B and across C ($k \neq k', l \neq l'$)	Sires	$s - 1$	$\frac{1}{n} \sum_i Y_{ikl} Y_{ik'l} - \frac{1}{n s} Y_{.kl} Y_{.k'l}$	$n C_{skk'l'l'}$
	Error	$s(n - 1)$	—	—

due to sires is

$$\begin{aligned}
 SS(S) &= \frac{1}{n b c} \sum_i Y_i^2 \dots - \frac{1}{n b c s} Y^2 \dots \\
 &= \frac{1}{n b c} \sum_i (Y_{i11} + Y_{i12} + \dots + Y_{ikl} + \dots + Y_{ibc})^2 \\
 &\quad - \frac{1}{n b c s} (Y_{.11} + \dots + Y_{.bc})^2 \\
 &= \frac{1}{n b c} \sum_i \left[\sum_k \sum_l Y_{ikl}^2 + \sum_k \sum_{l \neq l'} Y_{ikl} Y_{ik'l} \right. \\
 &\quad \left. + \sum_{k \neq k'} \sum_l Y_{ikl} Y_{ik'l} + \sum_{k \neq k'} \sum_{l \neq l'} Y_{ikl} Y_{ik'l'} \right] \\
 &\quad - \frac{1}{n b c s} \left[\sum_k \sum_l Y_{.kl}^2 + \sum_k \sum_{l \neq l'} Y_{.kl} Y_{.k'l} \right. \\
 &\quad \left. + \sum_{k \neq k'} \sum_l Y_{.kl} Y_{.k'l} + \sum_{k \neq k'} \sum_{l \neq l'} Y_{.kl} Y_{.k'l'} \right],
 \end{aligned}$$

and by comparing this to the expressions for sums of squares in Table 3, it can be seen that the expectation of mean squares due to sires is

$$\begin{aligned}
 EMS(S) &= \frac{1}{b c} \left[\sum_k \sum_l (V_{ekl} + n V_{skl}) \right. \\
 &\quad \left. + n(c - 1) \sum_k \sum_{l \neq l'} C_{skk'l'} \right. \\
 &\quad \left. + n(b - 1) \sum_{k \neq k'} \sum_l C_{skk'l} \right. \\
 &\quad \left. + n(b - 1)(c - 1) \sum_{k \neq k'} \sum_{l \neq l'} C_{skk'l'l'} \right].
 \end{aligned}$$

Doing similar algebraic manipulations for the other sources of variance of interest in Table 2 yields

$$\begin{aligned}
 EMS(S \times B) &= \frac{1}{b c} \left[\sum_k \sum_l (V_{ekl} + n V_{skl}) \right. \\
 &\quad \left. + n(c - 1) \sum_k \sum_{l \neq l'} C_{skk'l'} - \sum_{k \neq k'} \sum_l n C_{skk'l} \right. \\
 &\quad \left. - n(c - 1) \sum_{k \neq k'} \sum_{l \neq l'} C_{skk'l'l'} \right],
 \end{aligned}$$

$$\begin{aligned}
 EMS(S \times C) &= \frac{1}{b c} \left[\sum_k \sum_l (V_{ekl} + n V_{skl}) \right. \\
 &\quad \left. + n(b - 1) \sum_{k \neq k'} \sum_l C_{skk'l} - \sum_k \sum_{l \neq l'} n C_{skk'l'} \right. \\
 &\quad \left. - n(b - 1) \sum_{k \neq k'} \sum_{l \neq l'} C_{skk'l'l'} \right]
 \end{aligned}$$

and

$$\begin{aligned}
 EMS(S \times B \times C) &= \frac{1}{b c} \left[\sum_k \sum_l (V_{ekl} + n V_{skl}) \right. \\
 &\quad \left. - \sum_k \sum_{l \neq l'} n C_{skk'l} - \sum_{k \neq k'} \sum_l n C_{skk'l'} \right. \\
 &\quad \left. + \sum_{k \neq k'} \sum_{l \neq l'} n C_{skk'l'l'} \right].
 \end{aligned}$$

After defining

$$\bar{V}_{skl} = \sum_k \sum_l V_{skl} / b c,$$

$$\bar{C}_{sk(l)} = \sum_{k \neq k'} \sum_l C_{skk'l} / b c (b - 1),$$

$$\bar{C}_{s(k)l} = \sum_k \sum_{l \neq l'} C_{skk'l'l'} / b c (c - 1)$$

and

$$\bar{C}_{skl} = \sum_{k \neq k'} \sum_{l \neq l'} C_{skk'l'l'} / b c (b-1)(c-1),$$

it is an easy matter to show that

$$V_{sbc} = \bar{V}_{skl} - \bar{C}_{s(k)l} - \bar{C}_{sk(l)} + \bar{C}_{skl},$$

$$V_{sb} = \bar{C}_{s(k)l} - \bar{C}_{skl},$$

$$V_{sc} = \bar{C}_{sk(l)} - \bar{C}_{skl}$$

and

$$V_s = \bar{C}_{skl}.$$

Multiplying each of the among sire components of variance or covariance in Table 3 by four yields a function of an additive genetic or an additive genetic \times environmental component. Thus the numerator of the genetic correlation for the same trait averaged over both environmental classes B and C, obtained from the one-way analyses, is $4\bar{C}_{skl} = \bar{C}_{Akl} = 4V_s = V_A$, which is free of heterogeneity. The denominator of this genetic correlation from the one-way analyses is $\sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Akl} V_{Akl'}} / b c (b-1)(c-1)$, which is also unbiased by heterogeneity. Therefore unbiased genetic correlations derived from the one-way analyses of variance and covariance for the same trait are

$$r_G = \sum_{k \neq k'} \sum_{l \neq l'} C_{Akk'l'l'} / \sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Akl} V_{Akl'}}, \quad (4a)$$

$$r_{G(B)} = \sum_k \sum_{l \neq l'} C_{Akk'l'l'} / \sum_k \sum_{l \neq l'} \sqrt{V_{Akl} V_{Akl'}} \quad (5a)$$

and

$$r_{G(C)} = \sum_{k \neq k'} \sum_l C_{Akk'l'l'} / \sum_{k \neq k'} \sum_l \sqrt{V_{Akl} V_{Akl'}}. \quad (6a)$$

The correction for heterogeneity in r_G^* is the difference between the denominators of r_G and r_G^* . Thus the correction across levels of environments B and C for additive effects is

$$K_{ABC} = V_A + V_{AB} + V_{AC} + V_{ABC} - \sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Akl} V_{Akl'}} /$$

$$b c (b-1)(c-1) = \bar{V}_{Akl} - \sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Akl} V_{Akl'}} /$$

$$\begin{aligned} b c (b-1)(c-1) &= \frac{1}{b c (b-1)(c-1)} [(b-1)(c-1) \\ &\quad \cdot \sum_k \sum_l V_{Akl} - \sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Akl} V_{Akl'}}] \\ &= \frac{1}{b c (b-1)(c-1)} \sum_{k \neq k'} \sum_{l \neq l'} (\sqrt{V_{Akl}} - \sqrt{V_{Akl'}})^2 / 2. \end{aligned}$$

Similar reasoning gives the corrections for heterogeneity within B across C as

$$K_{A(B)C} = \frac{1}{b c (c-1)} \sum_k \sum_{l \neq l'} (\sqrt{V_{Akl}} - \sqrt{V_{Akl'}})^2 / 2$$

and within C across B as

$$K_{AB(C)} = \frac{1}{b c (b-1)} \sum_{k \neq k'} \sum_l (\sqrt{V_{Akl}} - \sqrt{V_{Akl'}})^2 / 2.$$

Thus the intraclass genetic correlations for the same trait corrected for heterogeneity are

$$\begin{aligned} r_G &= V_A / [(V_A + V_{AB} + V_{AC} + V_{ABC}) - K_{ABC}] \\ &= V_A / [V_A + (V'_{AB} + V'_{AC} + V'_{ABC})], \quad (4b) \end{aligned}$$

$$\begin{aligned} r_{G(B)} &= (V_A + V_{AB}) / [(V_A + V_{AB} + V_{AC} + V_{ABC}) - K_{A(B)C}] \\ &= (V_A + V_{AB}) / [(V_A + V_{AB}) + (V'_{AC} + V'_{ABC})] \quad (5b) \end{aligned}$$

and

$$\begin{aligned} r_{G(C)} &= (V_A + V_{AC}) / [(V_A + V_{AB} + V_{AC} + V_{ABC}) - K_{AB(C)}] \\ &= (V_A + V_{AC}) / [(V_A + V_{AC}) + (V'_{AB} + V'_{ABC})], \quad (6b) \end{aligned}$$

which respectively are equivalent to formulas (4a), (5a) and (6a). As the final form of these expressions indicate, the correlations can be viewed as a numerator variance divided by the numerator variance plus variance terms which must be corrected for heterogeneity. The prime on the variance components indicates that they have been corrected.

Solving a system of three equations gives the corrected variance components as

$$V'_{AB} = V_{AB} - K_{ABC} + K_{A(B)C},$$

$$V'_{AC} = V_{AC} - K_{ABC} + K_{AB(C)}$$

and

$$V'_{ABC} = V_{ABC} - K_{A(B)C} - K_{AB(C)} + K_{ABC}.$$

The K_{ABC} , $K_{A(B)C}$ and $K_{AB(C)}$ are all positive, being variances of standard deviations. However, their relative magnitudes are such that it is possible for the two-way interaction variance components to be biased downwards or upwards by heterogeneous variances. The V_{ABC} term is always biased upwards.

Factorial mating design

The concepts introduced in the previous section are now extended to a more complex genetic design with two environmental classes. The factorial mating design was described by Comstock and Robinson (1948). Sires and dams are randomly chosen for mating in a factorial arrangement. A sample of n full-sib progeny from each mating are assigned randomly to each of the $b c$ environmental subgroups. The statistical model is

$$\begin{aligned} Y_{ijkl} &= \mu + s_i + d_j + b_k + c_l + (s d)_{ij} + (s b)_{ik} + (s c)_{il} \\ &\quad + (d b)_{jk} + (d c)_{jl} + (b c)_{kl} + (s d b)_{ijk} + (s d c)_{ijl} \\ &\quad + (s b c)_{ikl} + (d b c)_{jkl} + (s d b c)_{ijkl} + e_{ijkl}. \end{aligned}$$

The term d_j is a random dam effect, $(s d)_{ij}$ is the interaction of sire i with dam j and the additional terms involving dam effects, $(d b)_{jk}, \dots, (s d b c)_{ijkl}$, are genotype \times environment interactions. All other effects were defined in the paternal half-sib model.

For brevity, the expected mean squares are presented only for the random model and the mixed model where both environmental factors are fixed (Table 4). As in the previous section, the random model will be used as a frame of reference. The equivalences of the variance components are

$$V_{sdbc} = V'_{sdbc}, \quad V_{sdb} = V_{sdb} - \frac{1}{c} V'_{sdbc},$$

$$V_{sdc} = V'_{sdc} - \frac{1}{b} V'_{sdbc}, \quad V_{sbc} = V'_{sbc}, \quad V_{dbc} = V'_{dbc},$$

$$V_{sb} = V_{sb} - \frac{1}{c} V'_{sbc}, \quad V_{db} = V_{db} - \frac{1}{c} V'_{dbc},$$

$$V_{sc} = V_{sc} - \frac{1}{b} V'_{sbc}, \quad V_{dc} = V_{dc} - \frac{1}{b} V'_{dbc},$$

$$V_{sd} = V_{sd} - \frac{1}{b} V'_{sdb} - \frac{1}{c} V'_{sdc} + \frac{1}{b c} V'_{sdbc},$$

$$V_s = V_s - \frac{1}{b} V'_{sb} - \frac{1}{c} V'_{sc} + \frac{1}{b c} V'_{sbc},$$

and

$$V_d = V_d - \frac{1}{b} V_{db} - \frac{1}{c} V_{dc} + \frac{1}{b c} V_{dbc}.$$

The factorial design produces paternal and maternal half-sibs and full-sibs grown in the same or different environmental levels of B and C. Using the covariances in Table 1 and omitting intermediate steps,

the causal variance components are

$$V_A = 4 V_s, \quad V_{A_m} + C_{AA_m} + V_{D_m} + V_{E_m} = V_d - V_s,$$

$$V_D = 4 V_{sd},$$

$$V_{AB} = 4 V_{sb}, \quad V_{A_m B} + C_{(AB)(A_m B)} + V_{D_m B} + V_{E_m B} \\ = V_{db} - V_{sb}, \quad V_{DB} = 4 V_{sdb},$$

$$V_{AC} = 4 V_{sc}, \quad V_{A_m C} + C_{(AC)(A_m C)} + V_{D_m C} + V_{E_m C} \\ = V_{dc} - V_{sc}, \quad V_{DC} = 4 V_{sdc},$$

$$V_{ABC} = 4 V_{sbc}, \quad V_{A_m BC} + C_{(ABC)(A_m BC)} + V_{D_m BC} + V_{E_m BC} \\ = V_{dbc} - V_{sbc} \quad \text{and} \quad V_{DBC} = 4 V_{sdbc}.$$

Assuming that V_{E_m} , V_{D_m} and all interaction variance components involving E_m and D_m are zero, the following maternal components are defined:

$$V_M = V_{A_m} + C_{AA_m}, \quad V_{M B} = V_{A_m B} + C_{(AB)(A_m B)},$$

$$V_{M C} = V_{A_m C} + C_{(AC)(A_m C)}$$

and

$$V_{M BC} = V_{A_m BC} + C_{(ABC)(A_m BC)}.$$

Any of these four components can have a negative expectation if the covariance part is negative and larger in absolute value than the variance part.

Additive genetic intraclass correlations for the same trait across environments, biased by heterogeneity, are obtained from formulas (1), (2) and (3). Analogously biased intraclass genetic correlations are defined for dominance effects as

$$r_D^* = V_D / (V_D + V_{DB} + V_{DC} + V_{DBC}), \quad (7)$$

$$r_{D(B)}^* = (V_D + V_{DB}) / (V_D + V_{DB} + V_{DC} + V_{DBC}) \quad (8)$$

Table 4. Analysis of variance and relevant expected mean squares for the factorial mating design with two environmental factors

Source	df	MS	Expected mean squares	
			Random model	B and C fixed
Env. B	$b - 1$	M_b		
Env. C	$c - 1$	M_c		
B \times C	$(b - 1)(c - 1)$	M_{bc}		
Sires (S)	$s - 1$	M_s	$V_e + n V_{sdbc} + n c V_{sdb} + n b V_{sdc} + n d V_{sbc}$	$V_e + n b c V'_{sd} + n d b c V'_s$
Dams (D)	$d - 1$	M_d	$V_e + n V_{sdbc} + n c V_{sdb} + n b V_{sdc} + n s V_{dbc}$ $+ n b c V_{sd} + n s c V_{db} + n s b V_{dc} + n s b c V_d$	$V_e + n b c V'_{sd} + n s b c V'_d$
S \times D	$(s - 1)(d - 1)$	M_{sd}	$V_e + n V_{sdbc} + n c V_{sdb} + n b V_{sdc} + n b c V_{sd}$	$V_e + n b c V'_{sd}$
S \times B	$(s - 1)(b - 1)$	M_{sb}	$V_e + n V_{sdbc} + n c V_{sdb} + n d V_{sbc} + n d c V_{sb}$	$V_e + n c V'_{sdb} + n d c V'_{sb}$
D \times B	$(d - 1)(b - 1)$	M_{db}	$V_e + n V_{sdbc} + n c V_{sdb} + n s V_{dbc} + n s c V_{db}$	$V_e + n c V'_{sdb} + n s c V'_{db}$
S \times C	$(s - 1)(c - 1)$	M_{sc}	$V_e + n V_{sdbc} + n d V_{sbc} + n b V_{sdc} + n d b V_{sc}$	$V_e + n b V'_{sdc} + n d b V'_{sc}$
D \times C	$(d - 1)(c - 1)$	M_{dc}	$V_e + n V_{sdbc} + n b V_{sdc} + n s V_{dbc} + n s b V_{dc}$	$V_e + n b V'_{sdc} + n s b V'_{dc}$
S \times B \times C	$(s - 1)(b - 1)(c - 1)$	M_{sbc}	$V_e + n V_{sdbc} + n d V_{sbc}$	$V_e + n V'_{sdbc} + n d V'_{sbc}$
D \times B \times C	$(d - 1)(b - 1)(c - 1)$	M_{dbc}	$V_e + n V_{sdbc} + n s V_{dbc}$	$V_e + n V'_{sdbc} + n s V'_{dbc}$
S \times D \times B	$(s - 1)(d - 1)(b - 1)$	M_{sdb}	$V_e + n V_{sdbc} + n c V_{sdb}$	$V_e + n c V'_{sdb}$
S \times D \times C	$(s - 1)(d - 1)(c - 1)$	M_{sdc}	$V_e + n V_{sdbc} + n b V_{sdc}$	$V_e + n b V'_{sdc}$
S \times D \times B \times C	$(s - 1)(d - 1)(b - 1)(c - 1)$	M_{sdbc}	$V_e + n V_{sdbc}$	$V_e + n V'_{sdbc}$
Error	$s d b c(n - 1)$	M_e	V_e	V_e

and

$$r_{D(C)}^* = (V_D + V_{DC}) / (V_D + V_{DB} + V_{DC} + V_{DBC}), \quad (9)$$

and for maternal effects as

$$r_M^* = V_M / (V_M + V_{MB} + V_{MC} + V_{MBC}), \quad (10)$$

$$r_{M(B)}^* = (V_M + V_{MB}) / (V_M + V_{MB} + V_{MC} + V_{MBC}) \quad (11)$$

and

$$r_{M(C)}^* = (V_M + V_{MC}) / (V_M + V_{MB} + V_{MC} + V_{MBC}). \quad (12)$$

To develop corrections for heterogeneity for formulas (7) to (12) requires extension of Table 3 to the two-way analyses of variance within environmental subclasses and analyses of covariance between environmental subclasses for the effects of sire, dam and sire \times dam interaction (Table 5). Deleting the intermediate steps, define \bar{V}_{skl} , $\bar{C}_{sk(l)}$, $\bar{C}_{s(k)l}$ and \bar{C}_{skl} as before and additionally

$$\bar{V}_{dkl} = \sum_k \sum_l V_{dkl} / b c,$$

$$\bar{C}_{dk(l)} = \sum_{k \neq k'} \sum_l C_{dkk'l} / b c (b-1),$$

$$\bar{C}_{d(k)l} = \sum_k \sum_{l \neq l'} C_{dkkl'l} / b c (c-1),$$

$$\bar{C}_{dkl} = \sum_{k \neq k'} \sum_{l \neq l'} C_{dkk'l'l} / b c (b-1)(c-1),$$

$$\bar{V}_{sdkl} = \sum_k \sum_l V_{sdkl} / b c,$$

$$\bar{C}_{sdk(l)} = \sum_{k \neq k'} \sum_l C_{sdkk'l} / b c (b-1),$$

$$\bar{C}_{sd(k)l} = \sum_k \sum_{l \neq l'} C_{sdkkl'l} / b c (c-1)$$

and

$$\bar{C}_{sdkl} = \sum_{k \neq k'} \sum_{l \neq l'} C_{sdkk'l'l} / b c (b-1)(c-1).$$

Now parameters in Table 4 can be defined in terms of parameters from Table 5 as

$$V_{dbc} = \bar{V}_{dkl} - \bar{C}_{d(k)l} - \bar{C}_{dk(l)} + \bar{C}_{dkl},$$

$$V_{db} = \bar{C}_{d(k)l} - \bar{C}_{dkl}, \quad V_{dc} = \bar{C}_{dk(l)} - \bar{C}_{dkl}, \quad V_d = \bar{C}_{dkl},$$

$$V_{sdbc} = \bar{V}_{sdkl} - \bar{C}_{sd(k)l} - \bar{C}_{sdk(l)} + \bar{C}_{sdkl},$$

$$V_{sdb} = \bar{C}_{sd(k)l} - \bar{C}_{sdkl}, \quad V_{sdc} = \bar{C}_{sdk(l)} - \bar{C}_{sdkl}$$

and

$$V_{sd} = \bar{C}_{sdkl}.$$

Noting that all terms containing the sire \times dam component or sire \times dam \times environment components are functions of one-fourth of a dominance component, we can write $4 \bar{C}_{sdkl} = \bar{C}_{Dkl} = 4 V_{sd} = V_D$ as the unbiased numerator of the dominance genetic correlation for the same trait averaged over both environmental factors. The unbiased denominator is

$$\sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Dkl} V_{Dk'l'}} / b c (b-1)(c-1).$$

Therefore, dominance genetic correlations for the same trait across one or two environments, unbiased by heterogeneity, are

$$r_D = \sum_{k \neq k'} \sum_{l \neq l'} C_{Dkk'l'l} / \sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Dkl} V_{Dk'l'}}, \quad (13a)$$

$$r_{D(B)} = \sum_k \sum_{l \neq l'} C_{Dkkl'l} / \sum_k \sum_{l \neq l'} \sqrt{V_{Dkl} V_{Dk'l'}} \quad (14a)$$

Table 5. Analyses of variance (ANOVA) within environmental subclasses and analyses of covariance (ANOCOVA) between environmental subclasses for the factorial design

Type of analysis	Source	df	EMS (CP)
ANOVA within B and C	Sires (S)	$s-1$	$V_{ekl} + n V_{sdkl} + n d V_{skl}$
	Dams (D)	$d-1$	$V_{ekl} + n V_{sdkl} + n s V_{dkl}$
	S \times D	$(s-1)(d-1)$	$V_{ekl} + n V_{sdkl}$
	Error	$s d (n-1)$	V_{ekl}
ANOCOVA across B within C ($k \neq k'$)	Sires (S)	$s-1$	$n C_{sdkk'l'l} + n d C_{skk'l'l}$
	Dams (D)	$d-1$	$n C_{sdkk'l'l} + n s C_{dkk'l'l}$
	S \times D	$(s-1)(d-1)$	$n C_{sdkk'l'l}$
	Error	$s d (n-1)$	—
ANOCOVA across C within B ($l \neq l'$)	Sires (S)	$s-1$	$n C_{sdkk'l'l} + n d C_{skk'l'l}$
	Dams (D)	$d-1$	$n C_{sdkk'l'l} + n s C_{dkk'l'l}$
	S \times D	$(s-1)(d-1)$	$n C_{sdkk'l'l}$
	Error	$s d (n-1)$	—
ANOCOVA across B and across C ($k \neq k', l \neq l'$)	Sires (S)	$s-1$	$n C_{sdkk'l'l} + n d C_{skk'l'l}$
	Dams (D)	$d-1$	$n C_{sdkk'l'l} + n s C_{dkk'l'l}$
	S \times D	$(s-1)(d-1)$	$n C_{sdkk'l'l}$
	Error	$s d (n-1)$	—

and

$$r_{D(C)} = \frac{\sum_{k \neq k'} \sum_l C_{Dkk'l}}{\sum_{k \neq k'} \sum_l \sqrt{V_{Dkl} V_{Dk'l}}} \quad (15a)$$

Similar reasoning leads to maternal components, e.g., $\bar{C}_{dki} - \bar{C}_{skl} = \bar{C}_{Mki} = V_d - V_s = V_M$, and unbiased maternal correlations for the same trait across one or both environments are

$$r_M = \frac{\sum_{k \neq k'} \sum_{l \neq l'} C_{Mkk'l}}{\sum_{k \neq k'} \sum_{l \neq l'} \sqrt{V_{Mkl} V_{Mk'l}}} \quad (16a)$$

$$r_{M(B)} = \frac{\sum_k \sum_{l \neq l'} C_{Mkk'l}}{\sum_k \sum_{l \neq l'} \sqrt{V_{Mkl} V_{Mk'l}}} \quad (17a)$$

and

$$r_{M(C)} = \frac{\sum_{k \neq k'} \sum_l C_{Mkk'l}}{\sum_{k \neq k'} \sum_l \sqrt{V_{Mkl} V_{Mk'l}}} \quad (18a)$$

Formulas (13a) to (18a) also can be expressed in terms of the variance components from the factorial analysis of variance in Table 4:

$$r_D = V_D / (V_D + V_{DB} + V_{DC} + V_{DBC} - K_{DBC}), \quad (13b)$$

$$r_{D(B)} = (V_D + V_{DB}) / (V_D + V_{DB} + V_{DC} + V_{DBC} - K_{D(B)C}), \quad (14b)$$

$$r_{D(C)} = (V_D + V_{DC}) / (V_D + V_{DB} + V_{DC} + V_{DBC} - K_{DB(C)}), \quad (15b)$$

$$r_M = V_M / (V_M + V_{MB} + V_{MC} + V_{MBC} - K_{MBC}), \quad (16b)$$

$$r_{M(B)} = (V_M + V_{MB}) / (V_M + V_{MB} + V_{MC} + V_{MBC} - K_{M(B)C}), \quad (17b)$$

and

$$r_{M(C)} = (V_M + V_{MC}) / (V_M + V_{MB} + V_{MC} + V_{MBC} - K_{MB(C)}) \quad (18b)$$

where

$$K_{DBC} = \frac{1}{bc(b-1)(c-1)} \sum_{k \neq k'} \sum_{l \neq l'} (\sqrt{V_{Dkl}} - \sqrt{V_{Dk'l}})^2 / 2,$$

$$K_{D(B)C} = \frac{1}{bc(c-1)} \sum_k \sum_{l \neq l'} (\sqrt{V_{Dkl}} - \sqrt{V_{Dk'l}})^2 / 2,$$

$$K_{DB(C)} = \frac{1}{bc(b-1)} \sum_{k \neq k'} \sum_l (\sqrt{V_{Dkl}} - \sqrt{V_{Dk'l}})^2 / 2,$$

$$K_{MBC} = \frac{1}{bc(b-1)(c-1)} \sum_{k \neq k'} \sum_{l \neq l'} (\sqrt{V_{Mkl}} - \sqrt{V_{Mk'l}})^2 / 2,$$

$$K_{M(B)C} = \frac{1}{bc(c-1)} \sum_k \sum_{l \neq l'} (\sqrt{V_{Mkl}} - \sqrt{V_{Mk'l}})^2 / 2$$

$$r_{G(BC)xy} = \frac{C_{AxAy} + C_{ABxABy} + C_{ACxACy} + C_{ABCxABCy}}{[(V_{Ax} + V_{ABx} + V_{ACx} + V_{ABCx})(V_{Ay} + V_{ABy} + V_{ACy} + V_{ABCy})]^{1/2}} \quad (22a)$$

and

$$K_{MB(C)} = \frac{1}{bc(b-1)} \sum_{k \neq k'} \sum_l (\sqrt{V_{Mkl}} - \sqrt{V_{Mk'l}})^2 / 2.$$

Genetic correlation between two traits

The genetic correlation between two traits X and Y is the correlation of breeding values for direct effects (Falconer 1981). Genetic correlations between traits averaged over environments or within environments were found by extending the concepts of the previous two sections. Analyses of variance across environments (Tables 2 and 4) and analyses of covariance between environmental subclasses (Tables 3 and 5) for the same trait were extended to analyses of covariance between two traits. The expected mean crossproducts were obtained in an identical manner. The additive genetic covariance component averaged across environmental factors B and C is

$$C_{AxAy} = 4 C_{s_x s_y} = 4 (\bar{C}_{s_x k l s_y k' l'} + \bar{C}_{s_x k' l' s_y k l}) / 2 \\ = (\bar{C}_{A_x k l A_y k' l'} + \bar{C}_{A_x k' l' A_y k l}) / 2.$$

Similarly, additive genetic \times environment covariance terms can be defined. Using these terms and analogous ones, the additive genetic correlation between two traits averaged over both environments is

$$r_{Gxy} = \frac{C_{AxAy}}{\sqrt{V_{Ax} V_{Ay}}} \quad (19a)$$

$$= \frac{\sum_{k \neq k'} \sum_{l \neq l'} (C_{A_x k l A_y k' l'} + C_{A_x k' l' A_y k l}) / 2}{\left[\left(\sum_{k \neq k'} \sum_{l \neq l'} C_{A_x k k' l l'} \right) \left(\sum_{k \neq k'} \sum_{l \neq l'} C_{A_y k k' l l'} \right) \right]^{1/2}} \quad (19b)$$

while the additive genetic correlations between two traits within B averaged over C, within C averaged over B, and with B and C are, respectively:

$$r_{G(B)xy} = (C_{AxAy} + C_{ABxABy}) / [(V_{Ax} + V_{ABx})(V_{Ay} + V_{ABy})]^{1/2} \quad (20a)$$

$$= \frac{\sum_k \sum_{l \neq l'} (C_{A_x k l A_y k' l'} + C_{A_x k' l' A_y k l}) / 2}{\left[\left(\sum_k \sum_{l \neq l'} C_{A_x k k' l l'} \right) \left(\sum_k \sum_{l \neq l'} C_{A_y k k' l l'} \right) \right]^{1/2}}, \quad (20b)$$

$$r_{G(C)xy} = (C_{AxAy} + C_{ACxACy}) / [(V_{Ax} + V_{ACx})(V_{Ay} + V_{ACy})]^{1/2} \quad (21a)$$

$$= \frac{\sum_{k \neq k'} \sum_l (C_{A_x k l A_y k' l'} + C_{A_x k' l' A_y k l}) / 2}{\left[\left(\sum_{k \neq k'} \sum_l C_{A_x k k' l l'} \right) \left(\sum_{k \neq k'} \sum_l C_{A_y k k' l l'} \right) \right]^{1/2}}, \quad (21b)$$

$$= \frac{\sum_k \sum_l C_{A_x k l A_y k l}}{\left[\left(\sum_k \sum_l V_{A_x k l} \right) \left(\sum_k \sum_l V_{A_y k l} \right) \right]^{1/2}} \quad (22b)$$

Equations (20a) to (22b) show that genetic correlations between two traits within environments are influenced by the magnitude of additive genetic by environment covariances and variances. The genetic correlation between two traits averaged over environments does not contain these effects (equations 19a and 19b). The genetic correlations between two traits are not affected by heterogeneity of genetic variances because the intraclass correlations (equations 19a to 22a) are equivalent to the interclass correlations (equations 19b to 22b), which are defined relative to the appropriate variances.

The genetic correlations due to dominance deviations and maternal deviations averaged across environmental classes B and C are easily derived from the relationships $C_{D_x D_y} = 4 C_{sd, sd_y}$, and

$$C_{M_x M_y} = C_{A_m, A_m_y} + C_{A_x A_m_y} + C_{A_y A_m_x} = C_{d_x d_y} - C_{s_x s_y}.$$

Therefore,

$$r_{D_{xy}} = \frac{C_{D_x D_y}}{\sqrt{V_{D_x} V_{D_y}}} \quad (23a)$$

$$= \frac{\sum_{k \neq k'} \sum_{l \neq l'} (C_{D_x k l D_y k' l'} + C_{D_x k' l' D_y k l})/2}{\left[\left(\sum_{k \neq k'} \sum_{l \neq l'} C_{D_x k k' l l'} \right) \left(\sum_{k \neq k'} \sum_{l \neq l'} C_{D_y k k' l l'} \right) \right]^{1/2}} \quad (23b)$$

and

$$r_{M_{xy}} = \frac{C_{M_x M_y}}{\sqrt{V_{M_x} V_{M_y}}} \quad (24a)$$

$$= \frac{\sum_{k \neq k'} \sum_{l \neq l'} (C_{M_x k l M_y k' l'} + C_{M_x k' l' M_y k l})/2}{\left[\left(\sum_{k \neq k'} \sum_{l \neq l'} C_{M_x k k' l l'} \right) \left(\sum_{k \neq k'} \sum_{l \neq l'} C_{M_y k k' l l'} \right) \right]^{1/2}} \quad (24b)$$

Dominance and maternal genetic correlations between two traits within environment B and(or) C follow directly as analogues of formulas (20a) to (22b).

Numerical example

A genotype by environment interaction study with beef cattle was conducted in North Carolina (Ahlschwede et al. 1969). Growth and body composition of yearling Hereford steers from different sires were studied using three fixed locations (B) and two fixed rations (C). The locations represented the Coastal plain (b₁), Mountain (b₂) and Piedmont (b₃) regions of North Carolina. At each location, individuals were fed either a corn-soybean ration in drylot (c₁) or were grazed on pasture (c₂). Progeny from each of 18 sires were randomly allocated to one of the location-ration subclasses.

A subsample of the data for final body weight and carcass fat content is used as an illustration of the paternal half-sib design. Two individuals were sampled from each sire-location-ration subclass to provide a balanced data set. Data were not adjusted for years, days on test or other environmental variables. Although not calculated, sampling variances of estimates are expected to be large because of the relatively small subsample of data. The example cannot be used to draw conclusions about the magnitude of genotype by environment interactions, the primary aim being to illustrate the methodology with actual data.

The analyses of variance and covariance based on the random model (Table 2) provided estimates of observational components which were multiplied by four to give causal components of variance and covariance for additive genetic and additive genetic by environment interaction effects (Table 6). One-way analyses of covariance (Table 3) yielded functions of additive components of covariance between environmental subclasses (Table 7).

Genetic correlations for the same trait (Table 8) were estimated by substituting the variance components from Table 6 into formulas (1) to (3). These genetic correlations are biased downward in absolute value by heterogeneity of genetic variances. Corrections for heterogeneity were found (Table 8) by substituting the appropriate covariances from Table 7 into the formulas for K_{ABC} , $K_{A(B)C}$ and $K_{AB(C)}$. Corrected estimates of the genetic correlations were obtained from formulas (4a) to (6a) and (4b) to (6b); these were numerically identical, as expected. The unbiased genetic correlations across locations and rations (r_G) and across locations within rations ($r_{G(C)}$) were similar for final weight, and also for carcass fat. If these genetic correlations are real they would be indicative of sizeable genotype by location interactions.

Table 6. Estimates of causal variance and covariance components for final weight and carcass fat content based on the analysis for the random model in the paternal half-sib design

Variance component	Trait		Covariance component	X, Y
	Final wt (X)	Carcass fat (Y)		
V_A	1099.67	1.0924	$C_{A_x A_y}$	-102.37
$V_{AB}(V_{AB}^a)$	2558.14 (2321.19)	13.6788 (16.1096)	$C_{AB_x AB_y}$	232.24
$V_{AC}(V_{AC}^a)$	551.59 (203.24)	-2.9880 (0.4064)	$C_{AC_x AC_y}$	-25.94
$V_{ABC}(V_{ABC}^a)$	-347.69 (-444.32)	14.4576 (4.2188)	$C_{ABC_x ABC_y}$	-11.43
Mean	413.55 kg	28.33%		
V_e	1617.19	14.09		

^a Interaction variance components in parentheses are adjusted for heterogeneity of genetic variances

Table 7. Estimates of causal components of variance and covariance between environmental subclasses for the paternal half-sib design

Final wt (X)		$C_{A,kk'l'l'}$; $k, k' = 1, 2, 3; l, l' = 1, 2$				
	11	12	21	22	31	32
11	8154.92	4573.72	6813.68	3588.24	- 843.28	- 589.72
12		3819.52	3035.00	2717.72	182.05	390.76
21			3953.36	3350.92	- 54.52	760.48
22				475.03	- 378.00	883.20
31					4147.25	3048.84
32						2620.22
Carcass fat (Y)		$C_{A,kk'l'l'}$; $k, k' = 1, 2, 3; l, l' = 1, 2$				
	11	12	21	22	31	32
11	11.6244	13.4048	7.2088	20.1556	- 23.4036	- 22.5992
12		10.4672	12.2896	22.4488	3.9456	- 4.8072
21			2.4072	11.8928	3.6244	10.3792
22				41.4688	- 17.6156	- 16.4432
31					72.3984	19.0016
32						19.0824
X/Y		$C_{A,k'lA,k'l'}$; $k, k' = 1, 2, 3; l, l' = 1, 2$				
	11	12	21	22	31	32
11	226.93	205.78	212.53	135.55	- 296.91	- 229.14
12	255.15	8.00	111.81	- 14.69	- 57.96	- 88.44
21	- 64.11	- 76.45	- 44.23	- 78.46	- 63.99	- 91.49
22	354.62	142.38	284.94	- 116.38	- 290.93	- 163.63
31	- 325.31	- 165.47	- 325.49	- 249.97	526.29	14.69
32	- 460.29	- 378.59	- 208.70	- 173.11	97.14	- 45.61

Table 8. Genetic correlation estimates for the same trait and for different traits across and within environments

Genetic correlation	Final wt (X)	Carcass fat (Y)	Genetic correlation	X, Y
$r_G^*(r_G)^a$	0.28 (0.51)	0.04 (0.05)	$r_{G_{xy}}$	- 2.95
$r_{G(B)}^*(r_{G(B)})$	0.95 (1.07)	0.56 (0.76)	$r_{G(B)_{xy}}$	0.56
$r_{G(C)}^*(r_{G(C)})$	0.43 (0.47)	- 0.07 (- 0.10)	$r_{G(C)_{xy}}$	^b
			$r_{G(BC)_{xy}}$	0.29
Corrections for heterogeneity				
K_{ABC}	681.94	4.4136		
$K_{A(B)C}$	445.74	6.8444		
$K_{AB(C)}$	333.58	7.8080		

^a Genetic correlations in parentheses are corrected for heterogeneity of genetic variances

^b Not estimable because of negative covariance component in the denominator

However the genetic correlation across rations within locations ($r_{G(B)}$) were larger for both traits. This indicates that genotype \times location interactions were larger than genotype \times ration interactions as noted in Table 6. The genetic correlation between final weight and carcass fat content, calculated from formulas (19a) to (22b), varied widely depending on whether it was calculated within or across locations and rations.

Discussion

In the present study we have derived the genetic correlation for one trait across two environmental factors and across one and within the other environmental factor. Correction factors were developed to yield genetic correlations and genotype by environment variance components that are unbiased by heterogeneity of genetic variances across environments. Expectations of additive genetic correlations between two traits across and within two environmental factors were derived and shown not to be biased by heterogeneity of genetic variances. The extension of the methods from two to multiple environmental classes is straightforward, unlike the case of going from one to two environmental classes. While we have not considered the sampling variances of the genetic correlations, previous studies indicate that large experiments will be required to obtain reliable estimates (Van Vleck and Henderson 1961; Klein et al. 1973).

We have defined both dominance and maternal genetic correlations and have shown how to estimate them from the factorial design. A more practical design for animals is the nested design where dams are nested

within sires. In this case, it is well known that the dam component is a pooled value of the dam and sire \times dam component of the factorial design. In traits which are primarily additive, the dam component in the nested design can be used to estimate the maternal genetic correlations.

Reviews of genotype \times environment interaction studies with animals generally suggest that the interactions are not large (Chapman 1968; Warwick 1972; Bowman 1972; Pani and Lasley 1972). Genotype \times environment interactions may be important where there are environmental extremes which induce stress conditions. These studies fail to reveal what can become apparent under the dynamics of selection. That is, apparent selection for an economic production trait may involve strong selection for genotypes performing well under the stress of exposure to disease or environmental extremes such as high temperature (Frisch 1981; Gavora et al. 1980).

Barlow (1981) has recently reviewed the evidence for interaction between heterosis and environment in plant and animal species and concluded that these interactions are the rule rather than the exception, particularly in stressful environments. One possible explanation is dominance by environment interactions. These interactions may more likely be present for traits associated with fitness. Genetic correlations due to dominance effects for the same trait across environments can be estimated from the factorial design.

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