Genetic Correlations and Maternal Effect Coefficients Obtained From Offspring-Parent Regression

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ABSTRACT

Additive genetic variances and covariances of quantitative characters are necessary to predict the evolutionary response of the mean phenotype vector in a population to natural or artificial selection. Standard formulas for estimating these parameters, from the resemblance between relatives in one or two characters at a time, are biased by natural selection on the parents and by maternal effects. We show how these biases can be removed using a multivariate analysis of offspring-parent regressions. A dynamic model of maternal effects demonstrates that, in addition to the phenotypic variance-covariance matrix of the characters, sufficient parameters for predicting the response of the mean phenotype vector to weak selection are the additive genetic variance-covariance matrix and a set of causal coefficients for maternal effects. These can be simultaneously estimated from offspring-parent regressions alone, in some cases just from the daughter-mother regressions, if all of the important selected and maternal characters have been measured and included in the analysis.

THE measurement of genetic correlations between characters is a common procedure in applied animal and plant breeding, and in the evolutionary genetics of natural populations. In both fields it is desirable to obtain estimates of genetic correlations in order to understand the hereditary constraints that influence the response of the mean phenotype vector to natural or artificial selection (HAZEL 1943; MAGEE 1965; YAMADA 1977; LANDE 1979). Genetic correlations may be calculated from the phenotypic resemblance among relatives, or from selection experiments (FALCONER 1981). However, deviations from the assumptions inherent in the use of standard methods can seriously alter the results. Either selection or non-Mendelian inheritance in the form of maternal effects can bias the traditionally calculated genetic correlations, producing estimates that are expected to deviate substantially from the true values (BROWN and TURNER 1968; VAN VLECK 1968; ROBERTSON 1977; MEYER and THOMPSON 1984; VAN NOORDWIJK 1984).

In this paper we focus on genetic parameters obtained from the resemblance between parents and their offspring. The genetic covariance between two characters may then be calculated either from the covariance of character one in the offspring with character two of the parents, or from the covariance of character two in the offspring with character one in the parents. These two measures of the offspring-parent covariance are usually combined by taking the arithmetic mean (REEVE 1955). Under normal Mendelian inheritance the two measures should be equivalent, apart from sampling error. The bias introduced by natural selection and/or maternal effects can cause the two measures of the genetic covariance to differ, however, depending on which character is measured in the parents and which in the offspring. A difference in the two offspring-parent covariances (which we term asymmetry), together with any difference in the covariances between offspring and each of the parents, can be used to correct standard calculations of genetic correlations to account for selection and maternal effects.

Although half-sib and full-sib analyses may be employed to estimate the additive genetic variance and covariance of the characters, they can not by themselves be used to correct for bias due to selection nor to estimate the parameters needed to predict the response to selection in the presence of maternal effects. This is because information on selection of parents, and which characters are maternally influencing offspring traits, is needed to accurately calculate heritabilities and genetic correlations, and to predict the response of the mean phenotype to individual selection (VAN VLECK 1968; ROBERTSON 1977; PONZONI and JAMES 1978; KIRKPATRICK and LANDE 1989).

Previous authors have estimated components of additive and dominance genetic variance and covariance, as well as maternal and environmental variance and covariance, using full and half sibs as well as other sets of relatives (*e.g.*, EISEN 1967; HANRAHAN and

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EISEN 1973; THOMPSON 1973, 1976; CHEVERUD *et al.* 1983; RISKA, RUTLEDGE and ATCHLEY 1985). Here we show how offspring-parent resemblance alone can be used to calculate the additive genetic variance-covariance matrix of the characters, **G**, and a matrix of causal coefficients describing maternal effects, **M**. In conjunction with the phenotypic variance-covariance matrix, **P**, and a vector of selection coefficients, these parameters are necessary and sufficient to predict the response to selection on correlated characters influenced by maternal effects, provided that all of the characters exerting maternal effects on the traits of interest are included in the analysis.

For a population with discrete, nonoverlapping generations and autosomal inheritance with no epistasis, KIRKPATRICK and LANDE (1989) derive the change in the mean phenotype vector, $\bar{\mathbf{z}}$, from generation t to generation $t + 1$ in response to weak selection as

$$\Delta\bar{\mathbf{z}}(t) = \mathbf{C}_{\mathbf{az}}\beta(t) + \mathbf{M}\{\Delta\bar{\mathbf{z}}(t - 1) + \mathbf{P}\Delta\beta(t - 1)\}. \quad (1)$$

$\mathbf{C}_{\mathbf{az}} = \mathbf{G}(\mathbf{I} - \frac{1}{2}\mathbf{M}^{\mathsf{T}})^{-1}$ is the covariance matrix of additive genetic and phenotypic values, in which **I** is the identity matrix and the superscript T indicates matrix transposition. $\beta(t) = \mathbf{P}^{-1}\mathbf{s}(t)$ is the selection gradient expressed in terms of the observed selection differential, $\mathbf{s}(t)$, the difference in the mean phenotype vector of selected and unselected parents in generation t. The selection gradient also can be measured as the vector of partial regression coefficients of individual relative fitness on the characters (LANDE and ARNOLD 1983).

We first analyze bias and asymmetry in genetic correlations produced by selection, and second, those produced by maternal effects. In each section we develop a general model, a specific example, and ways to correct for bias. We then analyze selection and maternal effects together. Throughout this paper we consider the covariances between offspring and parents to be population parameters; in the discussion we briefly review statistical methods that can be used to estimate additive genetic variances and covariances and maternal effect coefficients from samples.

SELECTION

General theory: Natural or artificial selection on the characters of parents will change their phenotypic variances and covariances and hence the offspring-parent covariances. This can bias estimates of genetic correlations. However, assuming that in the absence of selection the joint distribution of parental and offspring characters is multivariate normal, a result of PEARSON (1903) can be used to show that selection on the parents will not alter the partial regression coefficients in a multiple regression of offspring characters on parental characters, *provided that all of the selected characters are included in the regression.* This is the basis of the statement in ROBERTSON (1977) and FALCONER (1981, p. 169) that the heritability of a single character estimated from offspring-parent regression is not altered by selection on the parents (if selection acts only on that trait).

Denote the matrix of offspring-parent covariances as **C**, where the element C_{ij} is the covariance of character i in the offspring with character j in the parents before selection. In the following formulas this notation applies to either single parents (mothers or fathers) or midparents (the average of mother and father), assuming that the population mates at random, inheritance is autosomal, and there is no sexual dimorphism or sex-specific selection. The genetic correlation between characters i and j is traditionally obtained as $\gamma_{ij} = C_{ij}/\sqrt{C_{ii}C_{jj}}$ or $\gamma_{ji} = C_{ji}/\sqrt{C_{ii}C_{jj}}$.

Let **P** be the phenotypic variance-covariance matrix of characters in the parents before selection. The matrix of partial regression coefficients of offspring on parents in a hypothetical population without selection is $\mathbf{CP}^{-1}$. Using * to denote values after natural selection on parents, PEARSON's result is

$$\mathbf{CP}^{-1} = \mathbf{C}^*\mathbf{P}^{*-1}. \quad (2a)$$

This general result is consistent with any Mendelian and/or non-Mendelian mechanism of heredity (*e.g.*, maternal effects) that allows a multivariate normal distribution of parental and offspring phenotypes in the absence of selection. Thus the value of **C**, unaltered by natural selection on the parents, is

$$\mathbf{C} = \mathbf{C}^*\mathbf{P}^{*-1}\mathbf{P}. \quad (2b)$$

The matrix **C** is symmetric, apart from sampling error. However, the offspring-parent covariance matrix after selection on the parents, $\mathbf{C}^* = \mathbf{CP}^{-1}\mathbf{P}^*$, usually is not symmetric (see below).

To obtain an unaltered value of the offspring-parent covariance matrix before selection, **C**, from the observed matrix of offspring-parent partial regression coefficients after selection, $\mathbf{C}^*\mathbf{P}^{*-1}$, we need the phenotypic variance-covariance matrix in parents before selection, **P**. When this is not available, **P** can be approximated using the (unselected) offspring, assuming that the phenotypic variance-covariance matrix is nearly the same in parents before selection as in their offspring. If environmental sources of variability remain constant the phenotypic variance-covariance matrix for quantitative (polygenic) characters will not change greatly, over one generation even under strong selection (BULMER 1985, Chs. 9, 10; LANDE 1980).

Example: To assess the influence of selection on the parents in affecting genetic correlations computed from offspring-parent regressions, we analyze a simple example. Consider two correlated characters, only one of which is under direct selection, i.e. only one of

the characters is causally related to variation in fitness (LANDE and ARNOLD 1983). Let character 1 be under direct selection such that its phenotypic variance in the parents is reduced to a fraction $1 - k$ of that before selection, $P_{11}^* = (1 - k)P_{11}$. Then $P_{12}^* = (1 - k)P_{12}$ and $P_{22}^* = (1 - k\rho^2)P_{22}$ where ρ is the phenotypic correlation of the characters before selection (PEARSON 1903). Substituting these formulas into $\mathbf{C}^* = \mathbf{C}\mathbf{P}^{-1}\mathbf{P}^*$ we find that the offspring-parent covariance matrix after selection has the form

$$\mathbf{C}^* = \begin{pmatrix} (1 - k)C_{11} & C_{12} - kC_{11}P_{12}/P_{11} \\ (1 - k)C_{21} & C_{22} - kC_{21}P_{12}/P_{11} \end{pmatrix} \quad (3)$$

From this the two formulas for the genetic correlation between the characters after selection, under the assumption of Mendelian inheritance, are

$$\gamma_{12}^* = \frac{\gamma - k\rho h_1/h_2}{\sqrt{(1 - k)(1 - k\gamma\rho h_1/h_2)}} \quad (4)$$

$$\gamma_{21}^* = \frac{\gamma\sqrt{(1 - k)}}{\sqrt{(1 - k\gamma\rho h_1/h_2)}} \quad (5)$$

where γ is the true genetic correlation between the characters before selection, and h_1 and h_2 are, respectively, the square roots of the heritabilities of characters 1 and 2.

In general, both measures of the genetic correlation, and also their arithmetic or geometric average, are biased by selection. When the heritability of character 2 is low compared to that of character 1, it is possible for selection to cause the sign of γ_{12}^* to be opposite to that of the true genetic correlation. The two measures of the genetic correlation may have opposite signs, and their average may also have a sign opposite that of the true correlation. Selection on character 1 can cause one or both measures, or their average, to exceed 1.0 in magnitude. The most extreme effect of selection occurs when $k\gamma\rho h_1/h_2 > 1$ so that C_{22}^* is negative, implying a negative value of the heritability for character 2, which would occur under substantial selection when the characters are highly correlated and the heritability of the selected trait is much higher than that of the unselected trait. In this case, no calculation of the genetic correlation can be done from the offspring-parent covariances after selection, because the square root of a negative number is imaginary.

Inspection of these formulas shows that selection directly on character 1 in the parents creates an asymmetry (i.e. inequality) in the two measures of the genetic correlation, unless $\gamma = \rho h_1/h_2$. However, even in this special case of no asymmetry, both measures and their average are still biased by selection. Thus symmetry of measures of the genetic correlation does not necessarily indicate lack of bias. Numerical examples of bias and asymmetry are plotted as a function of the strength of selection in Figure 1 (see also BROWN and TURNER 1968; VAN VLECK 1968; MEYER and THOMPSON 1984).

MATERNAL EFFECTS

General theory: Maternal characters such as body size or care of the young can produce direct phenotypic effects on the offspring, distinct from genes transmitted by the parents. Maternal effects of this type are of widespread occurrence in animals and plants (CINDIFF 1972; ROACH and WULFF 1987). For simplicity, we assume that there is no direct phenotypic effect of fathers on offspring ("paternal effect"), so that there is only genetic transmission from fathers to the next generation. We also assume that the characters are autosomally inherited, that there is no epistasis or sexual dimorphism, and that the population mates at random, although the theory could be extended to cover more complex situations. The final assumption here, which is relaxed in the next section, is the absence of selection on parents or offspring. We show that, in addition to the well-known difference in offspring-mother and offspring-father resemblance, maternal effects can cause bias and asymmetry in genetic correlations obtained either from offspring-mother or from offspring-father covariances.

The phenotype vector of an individual before selection, $\mathbf{z}$, in a particular generation, $t + 1$, can be written as the sum of an additive genetic component, $\mathbf{a}$, an independent environmental component, $\mathbf{e}$ (including developmental noise and genetic dominance), and a component due to direct effects of the mother's phenotype in generation t,

$$\mathbf{z}(t + 1) = \mathbf{a}(t + 1) + \mathbf{e}(t + 1) + \mathbf{M}\mathbf{z}(t). \quad (6)$$

$\mathbf{M}$ is a matrix of maternal effect coefficients in which the element M_{ij} defines the strength of the maternal effect of character j in the mother on character i in the offspring, supposing that there is a linear relation between parent and offspring phenotype. The coefficient M_{ij} gives the change in offspring character i produced per unit change in maternal character j, holding constant the additive genetic value of offspring character i and the phenotypic values of all other maternal characters (KIRKPATRICK and LANDE 1989).

Denote the matrix of offspring-mother covariances as $\mathbf{C}^m$ where the element C_{ij}^m is the covariance of character i in the offspring with character j in the mother. Similarly, let $\mathbf{C}^f$ denote the offspring-father covariance matrix. KIRKPATRICK and LANDE (1989) derive the general formulas

$$\mathbf{C}^m = \tfrac{1}{2}\mathbf{G}(\mathbf{I} - \tfrac{1}{2}\mathbf{M}^\mathsf{T})^{-1} + \mathbf{M}\mathbf{P} \quad (7)$$

$$\mathbf{C}^f = \tfrac{1}{2}\mathbf{G}(\mathbf{I} - \tfrac{1}{2}\mathbf{M}^\mathsf{T})^{-1}. \quad (8)$$

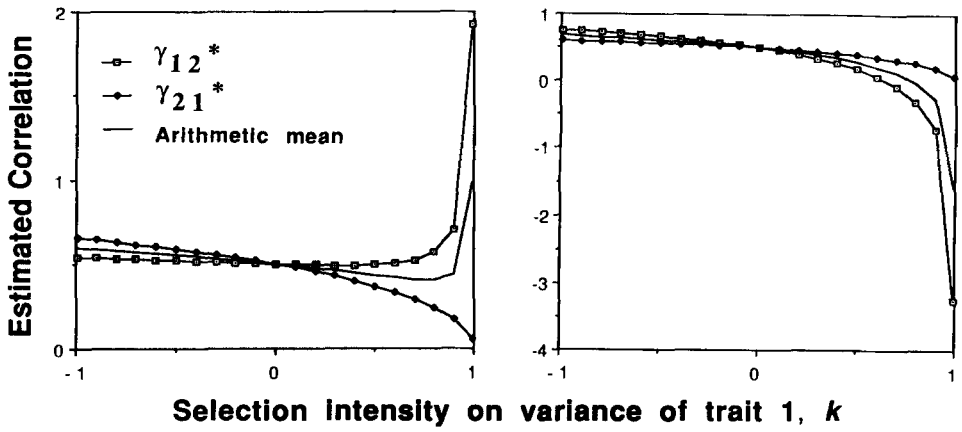

FIGURE 1.—Bias and asymmetry in the genetic correlation between characters caused by selection on the parents. Character 1 is under direct selection, and character 2 is not directly selected. k is the proportional decrease in the variance of character 1 caused by selection. Shown are the two values of the genetic correlation (γ_{12}^* from covariance of character 1 in offspring, 2 in parents; and γ_{21}^* from character 2 in offspring, 1 in parents), and their arithmetic mean, obtained from Equations 4 and 5 with $\gamma = 0.5$ and $\rho = 0.5$. (*Left*) $h_1^2 = 0.3$, $h_2^2 = 0.7$; (*right*) $h_1^2 = 0.7$, $h_2^2 = 0.3$. Note that the vertical axes of the two graphs are on different scales. The two values of the genetic correlation can be of opposite sign, and/or larger than 1.0 in magnitude.

The matrices of partial regression coefficients of offspring on mothers and fathers are, respectively, $\mathbf{C}^m\mathbf{P}^{-1}$ and $\mathbf{C}^f\mathbf{P}^{-1}$, and that for the offspring-midparent regression is the sum of these.

Neither $\mathbf{C}^m$ nor $\mathbf{C}^f$ is generally symmetric (see below). Therefore, even when using covariances of offspring with fathers, it should be expected that the two traditional measures of a genetic correlation for a pair of characters will be asymmetric, and that one or both, as well as their average, will be biased by maternal inheritance.

Unbiased values for genetic covariances and genetic correlations between characters can be obtained using a multivariate analysis of the offspring-mother and offspring-father covariances, *provided that all of the maternal characters influencing the characters of interest are measured and included in the analysis.* From Equations 7 and 8 the matrix of maternal effect coefficients **M** can be derived from the difference between the matrices of partial regressions of offspring on mothers and fathers,

$$\mathbf{M} = \mathbf{C}^m\mathbf{P}^{-1} - \mathbf{C}^f\mathbf{P}^{-1}. \quad (9)$$

Then, knowing **M**, the genetic variance-covariance matrix can be calculated from the offspring father covariances as

$$\mathbf{G} = 2\mathbf{C}^f(\mathbf{I} - \tfrac{1}{2}\mathbf{M}^T). \quad (10)$$

Sex-limitation of maternal characters, such as litter size and lactation performance in mammals, places severe restrictions on the application of this method, since the difference between offspring-mother and offspring-father regressions can not be taken if the character is not expressed in fathers. Partial sex-linked inheritance of the characters creates an inequality of offspring-mother and offspring-father covariances which would also invalidate the use of Equation 9. Nevertheless, even when some characters with maternal effects are sex-limited and/or partially sex-linked, if there are good reasons to assume that **M** is sparse, having mostly zero values, there may be sufficient information in the daughter-mother covariances to calculate the additive genetic variances and covariances of the characters and the nonzero maternal effect coefficients, as shown in the example below. For n characters in females, including the maternal traits, there are n^2 equations in the matrix Equation 7, and it is possible in principle to solve for the $n(n + 1)/2$ distinct additive genetic variances and covariances (since **G** is symmetric) in a model with up to $n(n - 1)/2$ nonzero maternal effect coefficients. However, this may be difficult in practice unless **M** has only a few nonzero elements, since otherwise the equations will be highly nonlinear.

Example: To assess the importance of maternal effects in biasing genetic correlations obtained from offspring-parent covariances, we analyze the following example. Consider a maternal trait (character 1), such as adult body size, that has a direct phenotypic effect on an offspring trait (character 2) such as fledgling or neonatal body weight, but no direct effect on itself (*i.e.*, offspring's adult body size). Thus let $M_{21} = m$ and let all other maternal effect coefficients equal 0. This model has been used extensively in the applied and evolutionary literature (DICKERSON 1947; WILLHAM 1963, 1972; CHEVERUD 1984; RISKA, RUTLEDGE and ATCHLEY 1985). The offspring-parent covariances take the form

$$\mathbf{C}^m = \begin{pmatrix} G_{11}/2 & G_{12}/2 + mG_{11}/4 \\ G_{12}/2 + mP_{11} & G_{22}/2 + mG_{12}/4 + mP_{12} \end{pmatrix} \quad (11)$$

$$\mathbf{C}^f = \begin{pmatrix} G_{11}/2 & G_{12}/2 + mG_{11}/4 \\ G_{12}/2 & G_{22}/2 + mG_{12}/4 \end{pmatrix} \quad (12)$$

in which the equilibrium phenotypic variances and covariance of the characters in the absence of selection

$$P_{11} = G_{11} + E_{11} \quad (13)$$

$$P_{12} = G_{12} + E_{12} + mG_{11}/2 \quad (14)$$

$$P_{22} = G_{22} + E_{22} + mG_{12} + m^2P_{11} \quad (15)$$

are given in terms of the genetic and the environmental covariances between characters, G_{ij} and E_{ij}, and the maternal effect coefficient, m (WILLHAM 1972; KIRKPATRICK and LANDE 1989).

It can be seen that maternal effects cause both of the offspring-parent covariance matrices to be asymmetric when the maternal character is heritable. WILLHAM (1963, 1972) and EISEN (1967) have previously shown that offspring-father covariances are influenced by heritable maternal effects. There are four possible ways of naively measuring the genetic correlation from offspring-parent covariances, which can be written as γ^m_{12} and γ^m_{21} for mothers and γ^f_{12} and γ^f_{21} for fathers. Each of these values, as well as any simple averages of them, generally will be biased with respect to the true genetic correlation, $\gamma = G_{12}/\sqrt{G_{11}G_{22}}$, although values from offspring-father covariances will be more accurate than those from offspring-mother covariances. In this model of maternal effects, bias cannot occur without asymmetry of the values obtained from parents of either sex. This model also shows that the two measures of the genetic correlation from mothers, or the two from fathers, may differ in sign, and that they and their averages may be greater than 1.0 in magnitude. In the extreme, it is not possible to evaluate the genetic correlation from maternal or paternal data if the calculated heritability of the offspring trait, character 2, has a negative value because C^m_{22} or C^f_{22} is negative.

Numerical examples of the biases and asymmetries caused by maternal effects are depicted in Figure 2.

If some characters are sex-limited, or if there is partial sex-linkage, then the daughter-mother covariances alone can be used to calculate the genetic correlation between the offspring and maternal traits. In this particular model there is sufficient information in the four daughter-mother covariances to obtain unbiased values for the two additive genetic variances, G_{11} and G_{22}, one additive genetic covariance, G_{12}, and the maternal effect coefficient m in females. Assuming that the phenotypic variances and covariances are known, the genetic and maternal effect parameters would be obtained in succession, first

$$G_{11} = 2C^m_{11}, \quad (16)$$

then from a pair of linear equations

$$m = (C^m_{21} - C^m_{12})/(P_{11} - G_{11}/4) \quad (17)$$

$$G_{12} = (2P_{11}C^m_{12} - \tfrac{1}{2}G_{11}C^m_{21})/(P_{11} - G_{11}/4) \quad (18)$$

and finally

$$G_{22} = 2C^m_{22} - mG_{12}/2 - 2mP_{12}. \quad (19)$$

COMBINED SELECTION AND MATERNAL EFFECTS

In many situations both selection and maternal effects act to alter offspring-parent covariances and the genetic correlations calculated by traditional methods. Matrices of offspring-parent covariances unaltered by selection on the parents can be obtained by applying PEARSON's result to mothers and fathers separately, $\mathbf{C}^m\mathbf{P}^{-1} = \mathbf{C}^m{}^*\mathbf{P}^{*-1}_m$ and $\mathbf{C}^f\mathbf{P}^{-1} = \mathbf{C}^f{}^*\mathbf{P}^{*-1}_f$. This allows selection to differ between the sexes. The method of Equations 9 and 10 can then be employed to derive the matrix of maternal effect coefficients, $\mathbf{M}$ and from this the additive genetic variance-covariance matrix, $\mathbf{G}$,

$$\mathbf{M} = \mathbf{C}^m{}^*\mathbf{P}^{*-1}_m - \mathbf{C}^f{}^*\mathbf{P}^{*-1}_f. \quad (20)$$

$$\mathbf{G} = 2\mathbf{C}^f{}^*\mathbf{P}^{*-1}_f\mathbf{P}(\mathbf{I} - \tfrac{1}{2}\mathbf{M}^T). \quad (21)$$

Again, even if some of the characters are sex-limited or partially sex-linked, there still may be sufficient information to obtain unbiased values of the additive genetic variances and covariances, and the maternal effect coefficients in females, from the daughter-mother regressions alone. This will be possible only if the matrix of maternal effect coefficients is assumed to be sparse, based on a particular causal model of development.

DISCUSSION

Genetic correlations between characters, calculated using standard formulas involving offspring-parent resemblance, can be altered from their true values by artificial or natural selection on the parents, and by maternal effects. Usually, such bias will show up in asymmetry of genetic correlations obtained from the covariance of character 1 in the parents with character 2 in the offspring, and *vice versa* (see Figures 1 and 2). In some cases, however, selection on the parents can bias the standard calculations of genetic correlations without producing asymmetry.

Strong selection on quantitative characters is not uncommon in natural populations (MANLY 1985; ENDLER 1986). For example, in a population of song sparrows reductions in phenotypic variance of up to 53% have been recorded in single periods of mortality (SCHLUTER and SMITH 1986a). Maternal effects, particularly on juvenile characters, also may be strong. From data in PRICE and GRANT (1985) and equations (11) and (12), we estimated the maternal effect of adult body size on hatchling body size in a population of Darwin's finches to be +0.6; a similar calculation for the same two traits in a population of great tits studied by VAN NOORDWIJK (1984) indicates m to be

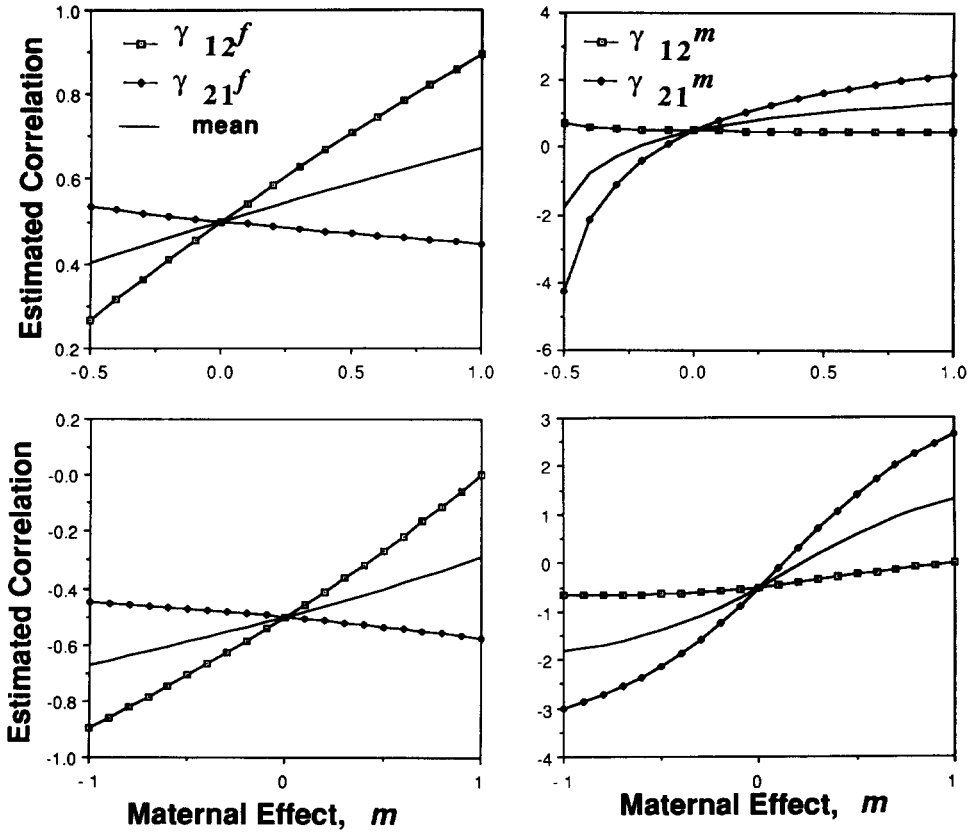

FIGURE 2.—Bias and asymmetry in the genetic correlation between characters caused by a maternal effect of character 1 in the mother on character 2 in the offspring. Shown, separately for offspring-father (*left*), and offspring-mother (*right*), are the two values of the genetic correlation (γ_{12}^f or γ_{12}^m from covariance of character 1 in offspring, 2 in parents; γ_{21}^f or γ_{21}^m from character 2 in offspring, 1 in parents), and their arithmetic mean, obtained from Equations 11 through 14, with $G_{11} = G_{22} = E_{11} = E_{22} = 1$, and $E_{12} = 0.5$. (*Top*) $G_{12} = 0.5$ (the genetic correlation is 0.5). (*Bottom*) $G_{12} = -0.5$ (the genetic correlation is −0.5). Note that the vertical axes of the graphs are on different scales. The horizontal axes also differ because, with the positive genetic correlation, a maternal effect less than −0.5 leads to a negative value of heritability in the offspring-mother regression.

approximately +0.3. FALCONER (1965) estimated in mice that the maternal effect of the mother's litter size on daughter's litter size was −0.13, and JANSSEN *et al.* (1988) found maternal effects as low as −0.5 for mother's age at maturity on daughter's age at maturity in a population of springtails. These values of k and m are of sufficient magnitude that we would expect serious bias to occur in traditional estimates of genetic correlations from natural populations (Figures 1 and 2). Indeed, VAN NOORDWIJK (1984) observed large, statistically significant asymmetries of offspring-parent covariances in a study of egg and body size characters in great tits, and SCHLUTER and SMITH (1986b) also found asymmetries in estimates of genetic correlations for morphological traits in song sparrows.

The maternal effects to which we refer are not expressed in terms of the usual components of phenotypic variance due to maternal influences (e.g. CHEVERUD *et al.* 1983; RISKA, RUTLEDGE and ATCHLEY 1985), but rather are coefficients describing the impact of particular maternal traits on offspring characters (Equation 6). Thus we have described methods for evaluating a more limited set of parameters than have previous authors who have been forced to consider several classes of relatives in complex breeding designs, because their goal was to exhaustively estimate all of the components of phenotypic variance, when the maternal character was not directly observed (EISEN 1967; THOMPSON 1976). Instead we assume that all of the maternal characters are measured and included in the analysis, and we derive only those parameters of inheritance and maternal effects needed to describe the response of the mean phenotype in a population to individual selection (Equation 1). We have demonstrated that, in a random mating population with no sex-dimorphism, knowledge of offspring-parent regressions and the phenotypic variance-covariance matrix before selection in the parents (or offspring) allows us to obtain unbiased values of the important parameters **G** and **M**. This may be possible even when some of the characters are sex-limited or partially sex-linked, or data on fathers are not available, if it is assumed that the matrix of maternal effect coefficients is sparse, with most of the entries being assigned zero values.

In natural populations parents and offspring may be the only relatives that can be identified with certainty. Often only the mother can be identified, and paternity is unknown or uncertain. Unbiased values of genetic correlations and maternal effects can be obtained most simply using only offspring-parent regression, provided that all selected characters correlated with those of interest, and all maternal traits influencing the characters of interest, are measured and included in the analysis. This multivariate approach differs from traditional methods for calculating heritabilities and genetic correlations between characters, which deal with only one or two characters

at a time (FALCONER 1981) and therefore can not generally produce values that are unbiased by selection and/or maternal effects.

The biases we have identified due to selection and maternal effects may be confounded with bias expected from random sampling errors. In maximum likelihood procedures, for example, there are at least two sources of such bias (SHAW 1987). One of these can be removed by the use of restricted maximum likelihood, but maximum likelihood methods and analysis of variance are biased by the common practice of disallowing negative variance components arising from sampling errors. Unless selection and maternal effects are properly corrected for, negative values for variance components may in some cases be expected. Maximum likelihood methods have been developed to account for selection effects and/or to estimate for a single character a maternal effect coefficient of the type considered here (THOMPSON 1973, 1976; MEYER and THOMPSON 1984; GRASER, SMITH and TIER 1987). It should therefore be possible to analyze the inheritance of multiple characters with more complex maternal effects using maximum likelihood.

Empirical workers may be reluctant to use the multivariate methods described above because of the absence of well-developed computerized statistical tests. Empirical standard errors for estimates of elements of **G** and **M** can be derived and statistical tests performed through the use of resampling techniques such as bootstrapping (EFRON 1982), or by employing maximum likelihood methods. Before using traditional formulas involving only single characters to estimate heritabilities, and pairs of characters to estimate genetic correlations, investigators should test for the existence of substantial selection and/or maternal effects which could seriously bias conventional estimates. Statistically significant selection coefficients (LANDE and ARNOLD 1983), or asymmetries in conventional estimates of genetic correlations obtained from offspring-parent resemblance, would indicate the need for a multivariate analysis.

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