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A Model for the Analysis of Mate Selection in the Marriages of Twins

*Application to Data on Stature**

W. E. Nance,¹ L. A. Corey,¹ L. J. Eaves²

¹Department of Human Genetics, Medical College of Virginia, Richmond; ²Department of Psychology, Oxford University

Analysis of the multiple correlations in body height within a sample of 117 monozygotic twin pairs and their spouses confirmed the existence of a high degree of assortative mating. However, the data also revealed an underlying asymmetry in the mate selection process. With respect to height, male twins were more selective than were members of female pairs, and among male twin pairs, those who were intermediate in height appeared to make the greatest contribution to the observed pattern of nonrandom mating. Because of their magnitude and potential asymmetry, the effects of phenotypic correlations between the spouses of related individuals must be correctly specified in any rigorous quantitative genetic analysis that extends beyond the nuclear family unit.

Key words: Mate selection, Sexual asymmetry, Stature, Marriages of twins, Twin-spouse correlation, Genetic model

INTRODUCTION

Since R. A. Fisher's pioneering work [6], assortative mating has traditionally been viewed as a homogeneous reciprocal process. However, common sense should warn us that the factors which influence mate selection may not be the same for males and females, and that, within a population, some genotypes may mate assortatively and others at random or even disassortatively. If bipolar assortment and/or sexual asymmetry in mate selection actually do exist for any trait, their effects could readily be detected by comparing the intraclass correlations of the multiple spouses in polyandrous and polygynous matings. Although the multiple causes of sequential polygamy in contemporary society have created many family units of this type, an analysis of the phenotypic correlations observed within the matings of male and female monozygotic (MZ) twins provide equivalent relationships which are not confounded by the potential social and psychological biases of serial marriages resulting from divorce or widowhood.

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GENETIC MODEL

Measurements on twins and their spouses permit the calculation of a maximum of six correlations for twins of each sex, which can be described by the genetic and environmental path diagrams shown in the Figure. For clarity and simplicity, we have elected not to include genetic environmental correlations in the model since Li has shown that, regardless of their magnitude, the ratio of the residual genetic and environmental effects remains constant [7]. The general model includes six genetic correlations, α_{ij} , β_i , δ_{ij} , and σ_i for the marriages of male ($i = 1$) and female ($i = 2$) twins, respectively, a total of 12 environmental correlations, τ_i , κ_i , μ_{ij} , ϵ_{ij} , and the standardized genetic and environmental path coefficients, h and c . Since the general model is clearly indeterminant, the reduced model shown in Table 1 is proposed. The first assumption of the reduced model postulates that the genetic correlation between MZ twins is unity. This would seem to be a reasonable approximation although it ignores the possibility of genetically determined cytoplasmic differences between MZ twins as well as variation resulting from Lyonization in female twins. The second restriction assumes that the genetic component of the marital correlation, α_{ij} , is the same for male and female twins, is equal to the genetic correlation between the spouse and cotwin, δ_{ij} , and does not differ with the birth order of twins. While all of these assumptions are plausible for identical twins, there is reason to question whether they would be valid for siblings or even for sequential marriages of an individual because of possible differences resulting from age, parity, primogeniture, or previous marital experiences. Our parameterization of the genetic component of the spousal correlation, σ_i , assumes that the transmitted genetic effect of marital assortment, a , is augmented by a sex-specific correlation, s_i , that arises from the tendency for twins to assort concordantly in their mate selection, as will be described in greater detail later. The environmental model assumes a pervasive kinship environmental correlation, k_i , which is augmented by u , the effect of a common home environment in the marital correlations, and t , the effect of the childhood environment and cultural inheritance of the twins. The restricted model assumes no difference in the twin and home environments of male and female twins and, as in the case of the genetic effects, does not admit the possibility of birth order effects. The assumptions given in Table 1 reduce to four the number of distinct correlations that can be derived from the marriages of twins of each sex. These are the twin-twin correlation, r_{TT} , the husband-wife or marital correlation, r_{HW} , the twin-spouse correlation, r_{TS} – that is, the correlation between one twin and the spouse of the cotwin – and the spousal correlation between the marriage partners of the twins, r_{SS} . The expected values of the eight correlations, along with the equation of determination, are shown in Table 2.

The relationship between the marital and spousal correlations deserves special comment. If a dichotomous phenotype is assumed, with twins and spouses simply being classified as above or below the population median, the direction – positive or negative – of the contribution of each mating to the overall marital and spousal correlations can readily be determined. If a proportion A of the marriages are assortative and D disassortative, then

$$A + D = 1, \quad (1)$$

and $A - D$ would be the average marital correlation in the population. The marriages of twins may be both assortative, AA , both disassortative, DD , one of each, AD , and if a random distribution is assumed, the three types would be expected to occur with frequencies

$$A^2 + 2AD + D^2 = 1. \quad (2)$$

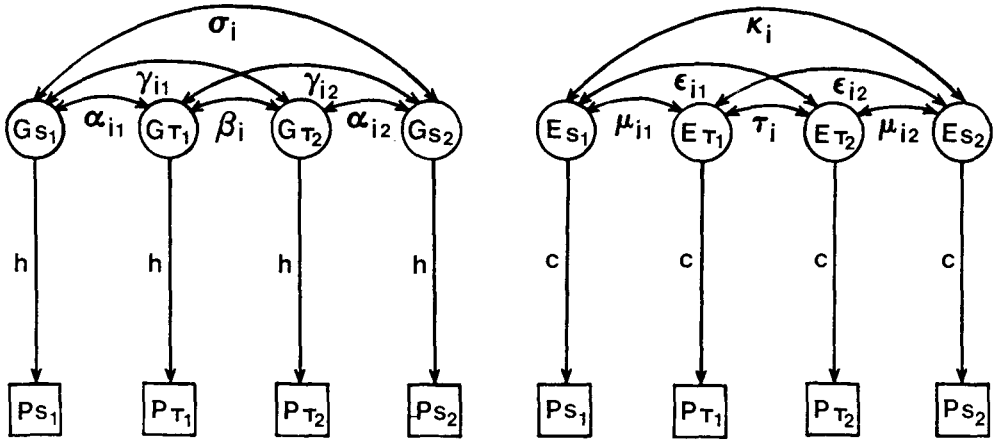


Figure. Path diagram showing genetic (left) and environmental (right) relationships between twins (T) and their spouses (S), where β and τ are the genetic and environmental correlations between twins, α and μ the genetic and environmental marital correlations, γ and ϵ the genetic and environmental correlations between spouse and cotwin, and σ and κ the genetic and environmental spousal correlations. The partial regression coefficients of genotype and environment on phenotype (P) are designated by h and c , respectively. The subscript i refers to the sex, and j to the birth order of the twins.

TABLE 1. Assumptions of Restricted Model

(1) $\beta_j = 1$	(4) $\tau_j = kM(F) + t$
(2) $\alpha_{ij} = \gamma_{ij} = a$	(5) $\mu_{ij} = kM(F) + u$
(3) $\sigma_i = a^2 + sM(F)$	(6) $\kappa_i = \epsilon_{ij} = kM(F)$

In a sample of married twins, the marital correlation will be given by

$$r_{HW} = A^2 - D^2 = (A + D)(A - D) = A - D, \tag{3}$$

which follows from equation 1 and the fact that the discordant mating types would have no net effect on the marital correlation. In contrast, both the concordant disassortative and concordant assortative twin mating types augment the spousal correlation while the discordant pairs diminish the correlation. Substituting from equation 3, we see that

$$r_{SS} = A^2 + D^2 - 2AD = (A - D)^2 = r_{HW}^2. \tag{4}$$

These relationships are illustrated in Table 3 where numerical values of A and D are given. The first line of the table shows that in a randomly mating population, where, by definition, half of the matings will be assortative and half disassortative, both the marital and spousal correlations will be zero. As the proportion of assortative matings in the population increases, it can be seen that the spousal correlation increases with the square of the marital correlation. However, this relationship will be valid only if the phenotypes of the twins are perfectly correlated: if they were uncorrelated, the spousal phenotypes would also be uncorrelated, no matter how similar the spouses were to their marriage partners.

TABLE 2. *Expected Values for Correlations Among Monozygotic Twins and Their Spouses*

Correlation	Expected value	
	Male twin kinships	Female twin kinships
r _{TT}	$h^2 + c^2(k_M + t)$	$h^2 + c^2(k_F + t)$
r _{HW}	$h^2a + c^2(k_M + u)$	$h^2a + c^2(k_F + u)$
r _{TS}	$h^2a + c^2k_M$	$h^2a + c^2k_F$
r _{SS}	$h^2(a^2 + s_M) + c^2k_M$	$h^2(a^2 + s_F) + c^2k_F$
Equation of determination: $1 = h^2 + c^2$		

k = Kinship environmental correlation; u = marital environmental correlation; t = twin environmental correlation; a = genetic assortative mating correlation; s = concordant mate selection correlation; h², c² = genetic and environmental variance.

Thus, the phenotypic correlation between the cognate relatives (in this case twins) acts to attenuate the expected value of the correlation between the spouses, as specified by the equation

$$r_{SS} = r_{TT}r_{HW}^2 \tag{4}$$

or, omitting genetic-environmental cross product terms,

$$r_{SS} = h^2\beta\alpha^2 + c^2\tau\mu^2. \tag{5}$$

In most circumstances, the predicted value of this correlation will be quite small. Even for MZ twins, where $\beta = 1$, the genetic component depends on the square of the genetic marital correlation while the environmental component is proportional to a third-order function of the primary environmental correlations. However, this formulation takes no account of the tendency for twins to assort concordantly in their mate selection. Consider, for example, a hypothetical population in which individuals are stratified with respect to a quantitative trait and randomly paired within strata to create “pseudo-twins” whose phenotypic correlation would then depend on the number of strata. If the original population was mating assortatively, one would expect a correlation between the spouses as predicted by equation 4, in spite of the fact that the phenotypic correlation between the pseudo-twins arises entirely from the artificial pairing rather than from a shared home environment or the possession of genes that are identical by descent. Because of their genetic identity or environmental similarities, real twins may tend to assort concordantly in their mate selection. This effect would lead to an increase in the AA and DD twin mating types in Table 3 at the expense of the AD class, which, if balanced (ie, bipolar assortment), could lead to a progressive increase in the spousal correlation as the intensity of concordant assortment increased while the marital correlation remained constant. Finally, even in the absence of any net evidence for assortative mating in the population (line 1, Table 2), the spouses of twins could still exhibit a positive correlation if it is assumed that some individuals tend to mate assortatively and others disassortatively and that biologic relatives are correlated with respect to this behavior.

In theory, concordant assortment could arise either from the shared genes or the shared environment of twins and could vary with their sex. In the model shown in Table 1, these possibilities are addressed by the inclusion of the sex-specific genetic and environmental

TABLE 3. Relation Between Marital and Spousal Correlations Without Concordant Assortment

Proportion of matings in general population	Expected proportion of twin mating combinations		Expected value of correlation	
	Assortative (A)	Disassortative (D)	r _{HW}	r _{SS}
0.50	0.50	0.50	AA - DD	(AA + DD) - AD
0.60	0.40	0.60	0.00	0.00
0.70	0.30	0.70	0.20	0.04
0.80	0.20	0.80	0.40	0.16
0.90	0.10	0.90	0.60	0.36
			0.80	0.64

correlations. The transmitted environmental effects of marital assortment, as well as the potential environmental similarities arising from concordant assortment, are assumed to be a form of social homogamy which contributes to, and is absorbed by, the environmental kinship correlations k_M and k_F . The genetic effects of concordant assortment are measured by s_M and s_F and can contribute to differences in the genetic correlations between the offspring of male and female twins. Further insight into the genetic and environmental causes of concordant assortment could be gained by the inclusion of offspring data or through an analysis of the marital and spousal correlations for other relationships such as fraternal twins or adoptive siblings.

The phenomenon of sexual asymmetry in mate selection can best be understood by considering an extreme case. Assume that women play a passive or indifferent role in mate selection for a given trait. Assume further that males, depending on their genotype, are predisposed to mate either assortatively or disassortatively and that the two types of males occur with equal frequency in the population. In this hypothetical situation the husband-wife correlation would be zero since there would be an equal proportion of assortative and disassortative matings. The correlation between the multiple husbands and polyandrous women would also be zero, since women would have an equal opportunity with every marriage of being selected by males who were mating either assortatively or disassortatively. On the other hand, the multiple wives of polygynous males would show a high intraclass correlation because of the postulated tendency of males to continue to mate either assortatively or disassortatively.

SUBJECT POPULATION

To illustrate the model, we have analyzed data on the body height of 119 pairs of MZ twins and their spouses, including 72 female and 47 male pairs. In each family, the zygosity of the twins was established by typing for 16 polymorphic systems. The sample included data on 86 MZ twin pairs that were gathered while the senior author was Principal Investigator of the Indiana University Human Genetic Center, while the remaining 33 pairs were studied at the Medical College of Virginia. Complete sets of observations on the twins and both spouses were available for 47 female and 43 male pairs. To remove the effects of sex differences in average stature, the raw height measurements were converted to standard scores with age-banded United States population norms [23]. The resulting scores were normally distributed, with a mean and variance which did not differ significantly from zero and one, respectively. The four distinct Pearsonian correlations were calculated for twins of each sex and are shown in Table 4. Since z transformation did not appreciably alter the magnitude of the correlations, untransformed correlations were used for subsequent analyses. The high twin-twin correlations, r_{TT} , agree with those observed in other samples of adult MZ twins [15] and are consistent with a major contribution of genetic factors to variation in stature. The husband-wife, r_{HW} , and twin-spouse correlations, r_{TS} , are comparable in magnitude, adumbrating a substantial degree of assortative mating with little evidence for a significant effect of adult home environment. Finally, although no major systematic difference is apparent in the magnitude of all the correlations derived from male in contrast to female twins, as might be expected with different kinship environmental effects, a substantial correlation, r_{SS} , was observed among the spouses of the male twins, but not among the spouses of the female twins, a finding which points to asymmetry in the mate selection process.

TABLE 4. Observed Correlations for Stature Among Monozygotic Twins and Their Spouses

Correlations	Male twins		Female twins	
	No. of pairs	Value of r	No. of pairs	Value of r
r _{TT}	47	0.931	72	0.922
r _{HW}	90	0.234	114	0.220
r _{TS}	90	0.218	114	0.216
r _{SS}	45	0.335	47	0.016

TABLE 5. Estimates of Genetic and Environmental Determinants of Stature Under Alternative Causal Models

Parameter	Causal model*			
	I	II	III	IV
h	0.962	0.962	0.962	0.962 ± 0.005
s _M	—	0.362	—	0.314 ± 0.105
s _F	—	0.017	—	—
a	—	—	0.239	0.238 ± 0.036
c	0.273	0.273	0.273	0.273
χ ²	24.59	19.75	4.96	0.167
df	7	5	6	5
p	<0.001	<0.002	0.549	0.999

*k_M = k_F = t = u = 0 in all models.

RESULTS

To obtain estimates of the genetic and environmental parameters of interest which utilize all of the available correlations simultaneously, a weighted least squares analysis was performed with a computer program which employed two minimization subroutines included in the IMSL statistical library. Using the expected values given in Table 1, we fitted various alternative solutions to the correlations. The results are summarized in Table 5. The first solution (I) shows that when a, s_M, s_F, k_M, k_F, t, and u were all set equal to zero, the simple genetic random environmental model failed to account adequately for the observed pattern of correlations as indicated by the large value of the goodness of fit χ². Since the estimate of s_F did not differ significantly from zero, model IV, in which only h, c, s_M, and a were estimated simultaneously while s_F was fixed at zero, yielded a parsimonious solution which fit the data extremely well. The inclusion of additional environmental parameters (ie, k, t, u) gave no further improvement of fit. In the final solution, genetic factors (h²) are estimated to account for 93% and random environmental effects (c²) for only about 7% of the total variance in stature. The pooled estimate of the genetic correlation between husbands and wives was 0.24, but the sex difference in the estimated degree of concordant assortment for male and female twins clearly suggests that assortative mating for stature arises largely from the phenotypic preferences of the male. To explore these effects further, we separately rank-ordered the male and female twins by mean height and partitioned the sample into equal-sized subgroups of tall, intermediate, and short twins. In Table 6, the results of an analysis of variance of the spouses' stature in the respective subgroups are given. The overall analysis provided evidence for significant variation among

TABLE 6. Analysis of Variance of Stature in the Spouses of Monozygotic Twins Classified by Mean Height of Twin Pair

Statistic	Tall		Intermediate		Short		Overall	
	Degrees of freedom	Value of statistic	Degrees of freedom	Value of statistic	Degrees of freedom	Value of statistic	Degrees of freedom	Value of statistic
Male Twins								
Among-pair mean square	13	0.82	14	2.53	13	0.58	42	1.36
Within-pair mean square	14	1.17	15	0.51	14	0.57	43	0.74
F		0.70		4.98		1.01		1.82
P		0.736		0.002		0.490		0.026
Twin mean (in SD)		+1.20		+0.25		-0.10		+0.24
Spouse mean (in SD)		+0.18		-0.26		-0.21		-0.09
Female Twins								
Among-pair mean square	15	0.96	14	1.05	15	1.07	46	1.12
Within-pair mean square	16	1.28	15	1.23	16	0.70	47	1.06
F		0.75		0.85		1.53		1.05
P		0.707		0.613		0.203		0.429
Twin mean (in SD)		+0.97		-0.18		-1.16		-0.24
Spouse mean (in SD)		+0.64		+0.21		+0.02		+0.29

the spouse pairs of male twins which was confined almost entirely to the spouses of twin pairs with intermediate stature. Among the female twins there was no evidence for genetically conditioned marital selectivity with respect to stature in either the overall or subgroup analyses.

DISCUSSION

Since 1972, it has been recognized that the families of identical twins contain a unique combination of distinct genetic relationships whose joint analysis permits an incisive resolution of genetic, environmental, and maternal effects [8]. Data from these families allow complex genetic models to be tested without the need either to combine heterogeneous bodies of data or to introduce environmental indices in order to achieve determinancy [9, 12]. This research design has subsequently been applied to the analysis of birth weight [13], dermal ridge count [10, 17], blood pressure [5, 20], serum cholesterol [1, 12], and uric acid levels [18], as well as several psychological traits [11, 19, 21, 22].

As noted elsewhere [9], data on the marriages of twins provide an unusual opportunity to partition the marital correlation into its causal elements as well as to detect concordant assortment and sexual asymmetry in the mate selection process [4, 14]. Marital correlations have frequently been attributed either to nonrandom mating or to the effects of a common home environment. In theory, they can arise from genetic assortment, from premarital or postmarital environmental similarities, or from some combination of these causes. In the present model, these effects can be resolved and are measured by the parameters a , k , and u , respectively.

Other models attempting to extend genetic analysis beyond the confines of the nuclear family have made no provision for the tendency of related individuals to assort concordantly in their mate selection and have thus yielded expected spousal correlations that are much lower than the empiric value we have observed for stature in the spouses of male twins [2, 3]. These formulations are also flawed by their failure to account for the potential effects of sex asymmetry in the mate selection process [16]. In the present model, the tendency for twins to assort concordantly is assumed to be either genetic or environmental in origin and is measured by the parameters s and k . Sex asymmetry in the intensity of marital selectivity can be detected by estimating separate values for these correlations in male and female twins. For stature, although a comparison of the z -transformed spousal correlations of male and female twins failed to show a statistically significant difference, an overall analysis of the entire set of correlations yielded an estimate of s_M that was more than twice its standard error and analyses of variance showed evidence for significant differences among the spouses of male twins but not female twins. Thus, although the data are not conclusive, they provide evidence both for concordant assortment and sexual asymmetry in mate selection for stature and illustrate how data on the marriages of twins can be used to detect these effects. An appropriate treatment of sex differences in mate selection is especially critical to any rigorous attempt to detect or measure maternal effects since asymmetry can either mask or mimic a true maternal effect by altering the relative magnitude of the maternal and paternal half-sib correlations [14]. Our data also demonstrate that even among males there is substantial heterogeneity in marital selectivity depending on their phenotypes. These effects could doubtless be incorporated into more elaborate models in which marital selectivity is specified as a function of the phenotype.

These results suggest that, to utilize the genetic relationships contained within extended pedigrees, it will be important to determine how the correlation between two spouses varies

with the genetic distance between their related marriage partners and whether the correlation is also influenced by differences in age, sex, or parity of the related marriage partners. None of these complexities enters into the analysis of data on the marriages of identical twins where the cognate relatives are always the same age and sex and their genetic relationship can be precisely specified. On balance, the use of stereotyped family structures such as these may prove to be a more tractable design for human genetic research on quantitative traits than the analysis of large, heterogeneous multigenerational pedigrees.

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Correspondence: Dr. W. E. Nance, Department of Human Genetics, Medical College of Virginia, Richmond, VA 23298.