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A Multivariate Genetic Analysis of Ridge Count Data From the Offspring of Monozygotic Twins

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Inheritance patterns of digital ridge counts have been analyzed using multivariate statistical methods and data from the offspring of half-sib twin kinships. Prior studies found the univariate measure total ridge count to be highly heritable and the counts on individual fingers to be somewhat less heritable, and exploratory factor analytic studies indicated that at least two, and possibly three, independent genetic influences are responsible for this ten variable multivariate trait.

Two statistical methods have been employed to elucidate the factors controlling ridge count development on all ten fingers. An exploratory method developed by Bock and Vandenberg [4] has been applied to the among and between mean square matrices from a multivariate nested analysis of variance on thirty balanced male twin kinships. A principal component analysis on the resulting matrix of pure genetic effects has revealed two substantial genetic factors. One strongly influences the counts on all ten fingers, with the largest loadings on the three central fingers of each hand, while the other has an impact on the thumbs and fifth fingers. For both factors the loadings on homologous fingers are nearly equal. This exploratory procedure is wasteful of the data that is available in half-sib twin kinships, however.

Confirmatory factor analyses, employing the LISREL IV program, have been conducted on all available ridge count data from the offspring of forty-eight unbalanced male twin kinships and fifty-nine unbalanced female twin kinships. Nested analyses of variance performed on sex-adjusted data yielded five 10×10 variance-covariance matrices containing 275 unique statistics for the estimation of genetic and environmental parameters and the testing of hypotheses.

A series of ten genetic and environmental hypothetical models for ridge count development, each more complex than the previous one, have been tested. They include a simple environmental model, an additive genetic and environmental model proposed by Holt [16], a full additive genetic model including five separate finger factors, two laterality factors and a general genetic factor, and seven models augmenting this full additive genetic model with factors for maternal epistatic and general environmental effects. The most complete model, which includes eight additive (one general, two laterality, and five finger) as well as maternal, epistatic, and general environmental factors cannot be rejected at a .05 level of significance. This model accounts for 99% of the variance that cannot be accounted for by a simple environmental model, and 95% of the variance unaccounted for by Holt's model. It suggests that while a strong genetic factor influences the ridge counts on all ten fingers, there are other factors affecting the counts on the homologous fingers separately as well as different factors affecting the counts on the left and right hands. In addition to these additive effects, influences due to the maternal environment common to all pregnancies of the mother, and those due to the unique environment of each pregnancy of the mother, and those due to the interaction of genes at separate loci have also been detected.

Results of the Bock and Vandenberg analysis are concordant with those obtained by the LISREL program. While the former only requires the availability of standard statistical packages, it is wasteful of data from the half-sib families. The latter, on the other hand, while it requires the use of a specific program, LISREL or its equivalent, uses all half-sibship data and allows one to test genetic and environmental hypotheses as well as conduct exploratory factor analyses.

Key words: Multivariate trait, Dermatoglyphics, Half-sib model, Finger ridge counts, Covariance structure analysis, Monozygotic twins

ABBREVIATIONS

V_P	*Population variance*
V_G	Genetic variance
V_E	Environmental variance
H^2	Broad heritability
V_A	Additive genetic variance
V_D	*Dominance variance*
V_{AA}	Epistatic variance
MZ	Monozygotic
DZ	Dizygotic
FS	Full siblings
HS	*Half-siblings*
V_M	Variance due to maternal effects
TRC	Total Ridge Count
Hp	Haptoglobin
PGM	Phosphoglucomutase
AP	Acid phosphatase
Hb	Hemoglobin
G6PD	Glucose-6-phosphate dehydrogenase
6PGD	6-Phosphogluconate dehydrogenase
C	Catalase
LDH	Lactic dehydrogenase
LT–L4	Fingers on the left hand (thumb to little finger)
RT–R4	Fingers on the right hand (thumb to little finger)

1. INTRODUCTION

A genetic analysis of continuously distributed human traits involves a resolution of the population variance (V_p) into its genetic and environmental components (V_G and V_E). The genetic variance is that caused strictly by genes, whereas environmental variance is generated by all other effects that modify the phenotype. The percentage of total variation attributable to genes has been termed the heritability (H^2) of a trait, and it is this portion of the variance that is of primary interest to the medical geneticist. The genetic variance, in turn, may be further partitioned into several components, the most important of which is that attributable to the additive effects of individual genes, two at each locus. One may conceive that the basis of an individual's phenotype is determined by the sum of small effects from each of the genes that influences it. The population variance due to these small effects is termed the additive genetic variance (V_A). Further variation in the population occurs through several other mechanisms. Dominance variance (V_D) is generated when, for at least one locus, the presence of one allele is sufficient to express the trait in question. Epistatic variance (V_{AA}) is generated when genes at one locus influence the contribution to the phenotype made by genes at another locus.

The resolution of phenotypic variation into its components may be accomplished through analyses of measurements on individuals who theoretically share specified fractions of their genes in common. For example, monozygotic (MZ) twins have identical genes, while dizygotic (DZ) twins and full siblings (FS) are expected to have one-half of their genes in common, and half-siblings (HS) one-fourth of their genes in common. Further, one may postulate that MZ and DZ twin pairs are affected by their environments in a similar manner. Each twin pair shares a certain set of common environmental influences which tend to keep them alike, whereas the individuals in each pair are also exposed to unique experiences which cause them to differ. In a twin analysis based on the preceding assumption, a comparison of within-pair differences for MZ and DZ twins may reveal genetic control of a trait. This is implied if the variance within DZ pairs is greater than that within MZ pairs. One may attribute the wider variation of the DZ pairs to the proportion of genes they do not share in common, and the greater similarity of the MZ twins to the fact that they have identical genotypes. Thus, one may infer that the expression of a trait is under genetic control if these intrapair differences are significantly different.

A form of analysis which is designed to permit more refined estimates of genetic and environmental parameters has been developed by Nance and Corey [34]. Their half-sib model involves the study of kinships consisting of a pair of monozygotic twins, their spouses, and their offspring as half-siblings sharing one-fourth of their genes. An analysis of variance on the full sibships nested within each half-sibship allows one to estimate additive, dominance, and environmental effects for the trait under consideration, as well as determine the presence of maternal effects (V_M), those factors which modify a phenotype and influence the offspring only through the mother.

A univariate half-sib analysis involves the estimation of five mean squares from nested analysesof variance on the offspring data measured on male and female twin kinships. Each mean square has as its expectation a linear combination of genetic and environmental components of variance, so that the final analysis involves the solution of five simultaneous equations. The inheritance patterns of a number of univariate quantitative traits have been investigated utilizing the half-sib model. Nance et al [35] have reported findings for diastolic and systolic blood pressures, total ridge count, birthweight, stature, serum cholesterol and immunoglobulin levels.

In addition to performing univariate analyses, it may be informative to study the variation in several quantitative traits simultaneously; that is, to consider the expression of a set of traits as one multivariate phenotype. This is especially warranted if one has evidence that individual variables are not independent but are associated through the pleiotropic effects of a set of genes. For example, gene expression on the right and left sides of the body may be considered bivariate. It has been found that anthropometric measures on adjacent parts of the body are often associated and may therefore be viewed as one multivariate trait. Associated risk factors for medical problems such as coronary heart disease too may be considered as multivariate, and behavioral research indicates that elements of intelligence and personality also display associations.

It is possible to detect the relationships in the phenotypic expression of a set of traits by performing a principal component analysis. Briefly, one takes measurements on a random sample of individuals, constructs a sum of squares and cross products matrix, and subjects the matrix to an eigenstructure analysis. This analysis allows one to determine a set of linear combinations of the traits under study such that the amount of variation for which each can account is maximized. These combinations are termed principal factors. If the traits exhibit groups of associations, each factor will be strongly influenced by only

a subset of the variables under analysis. The linear combinations of variables which determine the factors reveal the underlying phenotypic associations.

Often, the number of variables in a multivariate analysis may be reduced by a factor analytic procedure. The number of significant factors has been termed the dimensionality of the trait, and subsequent analysis with the factors rather than with the original variables reduces the number of elements under consideration. Factor analysis may thus be viewed as a procedure to simplify the study of a multivariate trait.

The dimensionality is more difficult to estimate for heritable variation than for phenotypic variation. This is because the phenotype of an individual may be determined directly up to the point of measurement error, whereas the genotype is masked by the influence of environment and is not directly measurable. In a simple univariate analysis, assuming no interactive genetic effects, one may estimate V_A by subtracting a mean square whose expectation is V_E from one whose expectation contains both V_A and V_E. For example, in an MZ-DZ twin analysis, the mean square within DZ twins, with an expectation of $1/2\ V_A + V_E$, less the mean square within MZ twins, with an expectation of V_E, yields an estimate of V_A. In a half-sib analysis, one may estimate V_A from the among component for males.

The mean sums of squares and cross products matrices cannot be subtracted from each other directly in a multivariate analysis as is done in the univariate case. The problem arises because the difference of two matrices will most often not conform to the specifications of a correlation matrix necessary for a factor analytic procedure. The essential criterion is that the matrix of differences be at least positive semidefinite. In 1968, Bock and Vandenberg [4] proposed a method for constraining the difference of two matrices to be at least positive semidefinite. Their result permits the estimation of a matrix of genetic effects which is suitable for factor analytic procedures. Nance et al [36] and Nakata et al [32] have utilized the procedure on MZ-DZ data sets to estimate the dimensions of heritability and sources of heritable variation for individual finger ridge counts and craniofacial measurements respectively.

A shortcoming of the Bock-Vandenberg procedure, however, is that it is wasteful of data, allowing the analysis of only one matrix estimate of V_A at a time. In addition, it is not possible to test for the presence or estimate the dimensions of variation in maternal or other environmental effects in a well-defined manner. These difficulties may be overcome, however, by employing the method of confirmatory factor analysis developed by Jöreskog [20] and adapted for the MZ-DZ model by Martin and Eaves [28]. When applied to half-sib data, it allows one to fit genetic and environmental models to a set of covariance matrices simultaneously and to explore the role of additive, epistatic, maternal, and environmental effects in the expression of given multivariate traits.

Confirmatory factor analysis has been employed in the solution of problems in fields as diverse as psychology, sociology, econometrics, and medicine. Basically, it is a procedure to derive maximum likelihood estimates of parameters in linear structural models and to test the goodness of fit of the proposed models. For a multivariate half-sib analysis, each sum of squares and cross products matrix is set equal to a linear combination of genetic and environmental latent variables according to the half-sib expectations, the factor analysis model, and the proposed model of genetic and environmental effects that are to be tested. More elaborate discussions of this procedure are provided in sections 2.3 and 3.3.c.

A multivariate trait that provides an excellent source of data through which to explore the multivariate half-sib model is that consisting of the ten individual finger ridge counts.

Ridged skin occurs on the palms, fingertips, toes, and soles of man and is composed of curved parallel lines of raised skin. Fingertip patterns are recorded from imprints of digits coated with printers ink and rolled across a sheet of paper. The finger patterns fall into three categories; arches, loops, and whorls. The pattern type is determined by the number of triradii present; a triradius being the junction of three regions, each containing parallel systems of ridges. Arches have zero triradii, loops one, and whorls two. In accordance with the work of Holt [16], ridge counts are determined by the number of ridges cut or touched by a straight line drawn from the triradius to the center of the pattern. The count for an arch is determined to be zero since no triradius exists, while that for a whorl is defined as the maximum of the two counts taken. Thus, a ridge count can be determined for each individual finger, yielding a multivariate trait of ten variables.

Prior research reports have facilitated our analysis of this trait. We expect to detect bilateral symmetry and the polygenic effects of a small number of genes for the ten ridge counts. Also, the ridge counts do not change with age, thus eliminating a complicated procedure of adjustment from the analysis. In addition, the absence of postnatal environmental effects on the trait, which is fully expressed at birth, permits us to attribute any significant environmental effects to the impact of environment early in the life of the fetus. A problem encountered in the analysis of this trait is that the large number of zero ridge count arches in the population skew the marginal distributions for each of the fingers, yielding a population that does not satisfy the assumption of multivariate normality. It is essential, however, that the procedures employed be robust against this deviation, as most sets of biological traits will probably not satisfy the assumption of multivariate normality.

The purpose of this study, therefore, is to apply and evaluate multivariate procedures for the analysis of half-sib data. In particular, the methods of Bock and Vandenberg [4] and the procedure of confirmatory factor analysis developed by Jöreskog [20] will be explored in depth using data on individual finger ridge counts.

2. LITERATURE REVIEW

2.1. Additive Procedures

The first analysis of the simultaneous effect of a locus or loci on several phenotypic traits was conducted by Tukey in 1951 [50]. On data from an experiment by Miller et al [30] in which protein levels were taken on four replications for each of nine single crosses of corn, he showed that the levels of lysine, methionine, tryptophane, and crude protein in maize are under the influence of one single genetically controlled factor. In this design, the expected values of mean squares within crosses are environmental effects ($W_{ij} = E_{ij}$), whereas those for mean squares between crosses are four times the genetic effects as well as those for environment ($B_{ij} = 4G_{ij} + E_{ij}$). Tukey therefore estimated the genetic effects by taking one-fourth the difference of the between and within mean squres [$G_{ij} = 1/4(B_{ij} - W_{ij})$]. Bock and Vandenberg [4] have used the term additive for this method and any procedure which estimates genetic effects through the direct difference of two mean squares.

In Tukey's study [50], a genetic component (G_{ij}) was estimated for each of the four protein levels individually, and in addition a mean cross product component was estimated for each of the pairwise combinations of the proteins. The resulting matrix of components was an expression of the multivariate genetic effects for protein levels in maize. Its correlation matrix, for which nearly all off-diagonal elements were close to one, suggested

that the same genetic factor was important in the control of all four protein levels. To verify this, Tukey extracted the first principal component from the genetic matrix and obtained a second matrix from the product of the component and its transpose. The corresponding entries of this estimated matrix and the original matrix were sufficiently close from observation to support the hypothesis of one strong genetic effect.

While the procedure described by Tukey is appropriate for the data examined in his analysis, its application is limited to only those traits which express the same genetic influence. A more refined methodology is required to detect the effects of more complicated genetic and environmental mechanisms.

Kempthorne and Osborne [24] introduced analysis of covariance into the genetics literature with the application of variance and covariance analysis to multivariate measures of height, weight, and ponderal index taken on MZ and DZ twin pairs. Four matrices of between pair variation for male and female MZ and DZ twins, taken separately, were constructed. The authors noted the similarity between the matrices and the fact that most of the variability was found to be between pairs and concluded that one common genetic factor accounted for a great deal of the variation and covariation in all three traits. Their findings were strictly observational, however, since no genetic components were estimated.

Loehlin and Vandenberg [27] used an additive procedure to analyze multivariate data from a set of MZ and DZ twin pairs in order to explore patterns of inheritance of cognitive abilities as determined by Thurstone's primary mental abilities test. Principal component analysis on a matrix of MZ twin differences followed by varimax rotation of the first five resulting factors from the raw data yielded four of Thurstone's five factors with the fifth factor suffering fragmentation. Since environment is the only source of MZ twin differences, the authors concluded that the five primary mental abilities reflect the structuring of environment on cognitive abilities. To detect the structuring of genetic effects on cognitive abilities, the authors analyzed a matrix of multivariate genetic effects, which was obtained by subtracting the MZ within pair variance-covariance matrix from the DZ within pair variance-covariance matrix after the MZ matrix had been corrected for attenuation. It was noted that one could not subtract the MZ matrix from the DZ matrix directly, since in most instances this difference could not be converted to a Gramian matrix because the variance due to measurement error was embedded in the entries of both matrices. A Gramian matrix is one with eigenvalues greater than or equal to zero. Further, this variance may be larger for some MZ entries than for the corresponding DZ entries, by chance yielding a negative difference. Correction for attenuation requires the estimation of measurement reliability and its use in the recalculation of the MZ matrix. Loehlin and Vandenberg [27] estimated the reliability of each subtest from the highest correlation involving that subtest. The matrix of genetic effects thus obtained was subjected to principal components analysis and rotated as in the analysis on environmental effects. Results indicated that the genetic structure of cognitive abilities is the same as that of environment. When the authors applied this methodology to the derived factor scores on Thurstone's five primary mental abilities, they found one common genetic factor influencing all five abilities. Although Loehlin and Vandenberg have extended from one to several the number of genetic factors that can be detected, the range of possibilities still remains quite limited for a multivariate trait.

2.2.a. The Bock and Vandenberg Procedure

Vandenberg [51] introduced a multiplicative procedure for determining a matrix of genetic effects which bypassed the problems inherent in the additive procedures used by Loehlin

[27], Tukey [50], and Kempthorne and Osborne [24]. This method involves the estimation of a matrix Θ of eigenvalues of $M^{-1}D$, a diagonal matrix into which $M^{-1}D$ had been transformed from MZ and DZ variance-covariance matrices (M and D respectively). With this transformation, the variances and covariances of $M^{-1}D$ could be explained by a set of independent factors. Vandenberg applied an approximate test for the number of significant eigenvalues (λ_l) developed by Bartlett [2] to estimate the dimensions of heritable variation in primary mental abilities data using a set of MZ and DZ twin pairs. In this analysis, four significant latent roots were detected, indicating at least four independent dimensions of heritable effects.

The test of Bartlett used by Vandenberg required the evaluation of

$$N_M + N_D - \frac{(N_D + p + 1)}{2}\left[\sum_{l=s+1}^{p} \log\left(1 + \frac{N_M}{N_D}\lambda_l\right)\right]$$

successively, each time eliminating the largest root until a nonsignificant χ^2 with $(p - s)(N_D - s)$ degrees of freedom was obtained. In this formula, N_M is the number of monozygotic twin pairs, N_D the number of dizygotic twin pairs, p the number of variables in the analysis, and s the number of roots eliminated. The largest value of s is an estimate of the dimension of heritable variation. Application of this test requires the assumption of multivariate normality.

In 1968, Bock and Vandenberg [4] employed the same procedure to estimate the dimension of heritable variation in another multivariate cognitive trait, differential aptitude test (DAT) scores, and then expanded upon their results to detect the corresponding sources of heritable variation. With univariate analyses, the authors were able to detect the presence of heritable variation for five of the eight subtests of the DAT for both male and female MZ and DZ twins. When Bartlett's [2] test was applied to the multivariate data, however, heritable variation was found in only three dimensions for males and two dimensions for females, indicating the existence of significant covariances between some of the tests.

When the procedure of Vandenberg [51] is applied to data, each latent root (λ_l) of the matrix $M^{-1}D$ may be employed to estimate the heritability of the dimension to which it corresponds using the formula

$$h_l^2 = r_l = \frac{\lambda_l - 1}{\lambda_l}$$

for dimension 1. To justify this interpretation, the following argument is employed: If one considers M as an estimate of environmental variance and covariance (E), and D as the sum of environmental and heritable variances (H + E), then one may denote eigenvalue λ_l of $M^{-1}D$ by $M^{-1}D_l$. Now, $r_l =$

$$\frac{\lambda_l - 1}{\lambda_l} = \frac{M^{-1}D_l - 1}{M^{-1}D_l} = \frac{E_l^{-1}(H_l + E_l) - 1}{E_l^{-1}(H_l + E_l)} = \frac{E_l^{-1}H_l + E_l^{-1}E_l - 1}{E_l^{-1}(H_l + E_l)}$$
$$= \frac{E_l^{-1}H_l + 1 - 1}{E_l^{-1}(H_l + E_l)} = \frac{H_l}{H_l + E_l} = h_l^2,$$

the heritability in dimension l.

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Once the dimension of heritable variation has been estimated, its sources can be determined provided a matrix of heritable effects Σ_H is estimated. To construct such a matrix, Bock and Vandenberg [4] employ the following argument:

Since M and D are both symmetric and positive definite matrices, there exists a nonsingular matrix transformation T such that $T' MT = I$ (a diagonal matrix with nonnegative elements) where $TDT = \Theta$. T is a matrix whose columns are eigenvectors of $M^{-1}D$ and the elements of Θ are their corresponding eigenvalues.

Now, $T' \Sigma_H T = \Theta - I$, so $\Sigma_H = (T^{-1})' (\Theta - I)T^{-1}$. Therefore, to obtain an estimate of Σ_H, one must employ the sample estimates of Θ and T from the eigenanalysis of $M^{-1}D$, and to ensure that Σ_H is at least positive semidefinite, the negative elements of $\Theta - I$ are set equal to zero. Bock and Vandenberg refer to this procedure as their correction for attenuation. It has been referred to by other authors as the Bock and Vandenberg procedure. In 1975, Bock and Petersen [3] proved that the procedure to correct for attenuation yields a constrained maximum likelihood estimate of the component covariance matrix.

Bock and Vandenberg have applied this procedure to the DAT data on MZ and DZ twin pairs and found that a large part of the heritable variation for all subtests of the DAT can be explained for both males and females by one common factor. They have also found a second factor of spatial abilities which accounts for more heritable variation in males than in females, and a third factor for clerical speed, which is present in both sexes.

2.2.b. Applications of the Bock and Vandenberg Procedure

Several applications of the Bock and Vandenberg procedure to MZ-DZ data have been reported. Nakata et al [31] analyzed thirty-three cephalometric measurements on 67 MZ and 29 like-sexed DZ twin pairs and found that the genetic covariances could be explained by at least nine independent significant heritable components. A large factor for mandibular length associated with cranial base dimensions, as well as eight other factors were identified. In addition to their analysis of heritable effects, the authors estimated and analyzed a matrix of environmental effects estimated from the difference of the within pair covariance and measurement error matrices, the second being generated by duplicate measurements on the same set of subjects. Sixteen significant environmental roots were found yielding eleven identifiable factors. However, the environmental factors did not parallel the genetic components in structure.

Nakata et al [32] analyzed 630 subjects for the thirty-three cephalometric measurements and subjected the resulting correlation matrix to varimax rotation. Nine significant factors were obtained, their structure differing from the heritable and environmental factors detected in a previous study. The authors concluded that, whereas a set of traits may be determined by a single genetic factor, this factor may be modified by more than one environmental influence. This phenomenon may account for the discrepancies in the structures of the factors.

Nance et al [36] reported on the application of the Bock and Vandenberg procedure to data on eight cephalometric measurements taken on 24 MZ and 21 like-sexed DZ twin pairs. Four significant independent dimensions of hereditary variation were detected for the cephalometric data. Dermatoglyphic variables, including ten individual finger ridge counts, left and right atd angles, a measure quantifying the position of the most distal axial triradius on the palm, and left and right proximal and distal triradial measurements were analyzed using the same procedure. Eight significant dimensions of heritable variation were found including four factors associated with individual finger ridge counts. These findings are discussed in greater detail in section 2.6.

Potter et al [40] applied the Bock and Vandenberg procedure to data on mesiodistal and buccolingual dimensions of 28 teeth of the secondary dentition for 43 pairs of MZ and 32 pairs of DZ twins. Four independent genetic factors influencing the size of the upper teeth and seven independent factors affecting the size of the lower teeth were found. A rotated factor analysis yielded several factors with homologous right and left measurements grouped together. For both maxillary and mandibular teeth, the genetic factors influencing them were found to be independent of each other.

2.3.a. Confirmatory Factor Analysis

Confirmatory factor analysis, as developed by Jöreskog [20], is one of the procedures associated with the general technique of covariance structure analysis, by which a variance-covariance matrix (Σ) is constrained to be of some particular structure and then analyzed. The general factor analytic model, upon which this is based, explains a given set of measured variables $x_1, x_2, \ldots x_p$ by a set of underlying latent factors $f_1, f_2, \ldots f_k$. The latent and measured variables are related by the linear model $x = \mu + \Lambda f + z$ where $z_1 \ldots z_p$ are trait specific residuals beyond that accounted for by $f_1 \ldots f_k$. $E(x) = \mu$, $E(f) = 0$, and $E(z) = 0$, and z is uncorrelated with f. If one lets $\Theta = E(ff')$, a correlation matrix, and $\Psi = E(zz')$, then the covariance matrix of x becomes: $\Sigma = \Lambda\Theta\Lambda' + \Psi$, where the dimensions Σ, Λ, Θ, and Ψ are pxp, pxk, kxk, and pxp, respectively. One is allowed to specify any parameters in the Λ, Θ, and Ψ matrices in advance while the rest are estimated by the method of maximum likelihood. The goodness of fit of a proposed factor analytic model is then tested by the likelihood ratio statistic.

Jöreskog [20] describes his procedure for confirmatory factor analysis as similar to those reported in the earlier works by Howe [17], Anderson and Rubin [1], Lawley [25], and Jöreskog [19]. His procedure is more general, however, in that it permits factors to be orthogonal, oblique or a mixture of the two, while the fixed variables can be values other than zero. For the factor analytic model, if the input vector x follows a multivariate normal distribution, then the elements of its variance-covariance matrix follow a Wishart distribution with $n-1$ degrees of freedom, where n is the number of multivariate observations in the analysis. The log likelihood of the observed covariance matrix S given Σ and neglecting a constant function of the observations is

$$\log L = 1/2(n-1)\,[\log\Sigma + \mathrm{tr}(S\Sigma^{-1})].$$

In the above expression, when the alternative to the proposed model is the perfectly fitting covariance structure S, we have $\Sigma = S$ with $\mathrm{tr}\,(S\,\Sigma^{-1}) = p$, where log S and p are both constant functions of the data. The likelihood ratio test statistic of the proposed model compared to the perfectly fitting model is then

$$L = -1/2(n-1)\,[\log\Sigma + \mathrm{tr}(S\Sigma^{-1}) - \log S - p].$$

Maximizing this statistic is equivalent to maximizing the original log likelihood because $\log|S|$ and p are constant values. Jöreskog, however, prefers to minimize the simplified expression

$$F(\Lambda, \Theta, \Psi) = \log\Sigma + \mathrm{tr}\,(S\Sigma^{-1}) - \log S - p,$$

the likelihood ratio test statistic multiplied by $-2/(n-1)$, which yields an equivalent set of estimates. His minimization procedure, based on the method of Fletcher and Powell [11], is a rapidly converging iterative procedure for minimizing a function of several variables when analytical expressions for the first-order derivatives are available. Lawley and Maxwell [26], and Jöreskog [19] determined the expressions for the first-order derivatives of F, thus permitting use of the Fletcher-Powell algorithm. They showed that:

$$\partial F/\partial \Lambda = 2\Sigma^{-1}(\Sigma - S)\,\Lambda\,\Theta$$

$$\partial F/\partial \Theta = c\Lambda'\Sigma \quad \Lambda^{1} \quad \begin{cases} c = 1 \text{ for diagonal elements} \\ c = 2 \text{ for off-diagonal elements, and} \end{cases}$$

$$\partial F/\partial \Psi = \text{diag}[\Sigma^{-1}(\Sigma - S)\Sigma^{-1}]$$

where the entries corresponding to any fixed values on the left are zero. In Jöreskog's procedure, the first few iterations are computed by the method of steepest descent, which usually brings one into the neighborhood of the minimum. The Fletcher-Powell algorithm is then applied. A detailed discussion of this procedure is presented in the 1969 paper by Jöreskog [20] on confirmatory factor analysis.

In 1971, Jöreskog [21] reported on a procedure to perform confirmatory factor analysis on several populations simultaneously, which is an extension of the single population procedure described in 1969, but allows one to work with several independent input variance-covariance matrices in the same analysis, as long as they are derived from well-defined populations. In the case where there are several populations, the likelihood function for each individual group is the same as that for the single group analysis. Since the groups are independent, when they are taken simultaneously the expression for their entire log likelihood becomes:

$$\text{Log } L = \sum_{g=1}^{m} \log(L_g),$$

where m is the number of groups in the analysis. As in the single group analysis, Jöreskog prefers to minimize the equivalent function:

$$F = \sum_{g=1}^{m} \frac{N_g}{N} [\log|\Sigma^g| + \text{tr}(S^g(\Sigma^g)^{-1}) - \log|S^g| - p]$$

where N_g is the number of observations in group g,

$$N = \sum_{g=1}^{m} N_g$$

and Σ^g and S^g are the proposed and observed covariance matrices in population g.

Under the assumption of multivariate normality, the goodness of fit of a proposed factor analytic model has a large sample chi square distribution. For a single population, the negative of twice the logarithm of the likelihood ratio of the proposed model to the model which fits perfectly is $(N - 1)F^*$ where F^* is the minimum value of F, and N is the sample size. This is distributed asymptotically as χ^2 with $d = 1/2(p)(p + 1) - t$ degrees of freedom, where t is the total number of independent parameters in the model being tested. For multiple populations, the goodness of fit statistic is defined as above with the degrees of freedom $d = 1/2(p)(p+1)m - t$, where m is the number of groups in the analysis and t is the total number of independent parameters estimated in all of the groups.

A desirable feature for a factor analytic model is that it be identified. That is, if several sets of parameter estimates for Λ, Θ, and Ψ all generate the same Σ, then every parameter

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has the same value across all sets. In other words, the parameter estimates for a given Σ must be unique. Only when these estimates are consistent is it meaningful to evaluate the model. The identification problem is usually solved by fixing or constraining a sufficient number of parameters. A detailed discussion of the identification of models is provided in Fisher [10].

2.3.b. Applications of Confirmatory Factor Analysis to Research in Human Genetics

The procedure of confirmatory factor analysis has been employed in several studies involving MZ and DZ twins to investigate the inheritance patterns of sets of psychological traits. The most informative was an article written by Martin and Eaves [28] in which an excellent description of the application of Jöreskog's techniques to data on twin pairs was given. They analyzed Thurstone's five primary mental abilities using the same data set as that discussed by Loehlin and Vandenberg in 1968 [27]. Input for their analysis consisted of four matrices of mean squares and cross products from analyses of variance on the MZ and DZ twin pairs. Expectations of each of these observed matrices are as follows:

$$
\begin{aligned}
E(S_{BMZ}) &= \Delta\Delta' + D^2 + HH' + E^2 \\
E(S_{WMZ}) &= HH' + E^2 \\
E(S_{BDZ}) &= 3/4\,(\Delta\Delta' + D^2) + HH' + E^2 \\
E(S_{WDZ}) &= 1/4\,(\Delta\Delta + D^2) + HH' + E^2
\end{aligned}
$$

where S_{BMZ}, S_{WMZ}, S_{BDZ} and S_{WDZ} are the sums of squares and cross products matrices between and within MZ twins and between and within DZ twins respectively, and where Δ is the matrix of additive genetic loadings, H is the matrix of within family environmental loadings, D^2 is the diagonal matrix of specific additive genetic variances, and E^2 is the diagonal matrix of specific within family environmental variances. Maximum likelihood estimates of parameters in proposed models of inheritance were obtained using subroutine EO4HAF of the Numerical Algorithms Group package [37]. The minimizaiton procedure employed the Powell-64 method where numerical approximations to the first derivatives of the likelihood function with respect to the parameter estimates are used.

Initially, the authors fit a simple additive genetic (D_R) and within family environmental (E_1) model to the data. It failed badly ($\chi^2_{40} = 72.5$, $p < .001$). A model containing between family environmental (E_2) and within family environmental factors also failed ($\chi^2_{40} = 127.5$). A combination of these models containing E_1, E_2 and H_R fit very well, ($\chi^2_{30} = 33$). The authors cautioned that one should view these results carefully, as they must be interpreted only with an understanding of the assumptions underlying the twin method. That is, for example, if assortative mating is occurring for that trait and the population is in equilibrium, E_2 is in fact $E_2 + \frac{1}{2}A/(1 - A)$, where A is the correlation between breeding values of the spouses. Their test of a model containing a parameter for assortative mating failed to fit, and the authors, therefore, retained the model with general and specific factors for E_1, E_2, and D_R. Their final analysis of the data included a breakdown of the total variation explained by the general and specific factors. They found that 69.9% of the variation in numerical ability could be accounted for by additive genetic variance, whereas variance due to the environment between families accounted for 16.5%. Similar partitions of variation in the other four traits indicated high heritabilities for word fluency and verbal comprehension.

Eaves et al [9] followed the study on mental abilities with one designed to study four aspects of impulsiveness as measured by Eysenck's personality questionnaire. A difference in design between this and the previous study was that the possibility of sex limitation was explored. Initially, data on the sexes were combined and a simple additive genetic and random environmental model was proposed. As an added constraint, each parameter in the matrix of environmental factor loadings was fixed to be a constant multiple of the corresponding loading on the additive genetic factor. The proposed model fit the data, but the authors considered the associated p value of .09 to be relatively poor. They, therefore, relaxed the constraint on the environmental loadings and the fit of the model improved slightly, with the associated p value rising to .142. Separate analyses on the male and female twin pairs indicated that the genetic determinants of trait specific variation were different in the two sexes. A single model containing different specific variances for males and females fit well ($\chi^2_{83} = 88.5$, $p = .319$) and was significantly better than the model which treated observations on males and females as equivalent.

Fulker [12] has provided a comprehensive review of the literature on multivariate analyses of twin data and has discussed the methods of Tukey, Bock and Vandenberg, and Jöreskog, as well as some of their applications. In addition, he has reported on a multivariate study of data on sensation seeking which was similar in design to the study on impulsiveness by Eaves et al. [9] He fitted a model to the data they had used, but this one included factors for additive by environmental interactions. Initially, he estimated entire component matrices for these effects and then, upon observation, was able to reduce the number of estimated parameters for each of the component matrices. His findings for sensation seeking behavior were similar to those of Eaves et al for impulsiveness, except that in this case, sex differences were explained by an interaction between genotype and sex.

In 1979, Martin et al [29] analyzed data from MZ and DZ twin pairs on impulsiveness, sensation seeking, and Eysenck's principal personality dimensions. As in previous studies, the methods of maximum likelihood confirmatory factor analysis were employed. In all, there were 12 variables measured on 231 MZ twin pairs and 188 DZ twin pairs. Tests of several plausible hypotheses yielded inadequate fits to the data. The authors pointed out that significant lack of fit to reasonable models is a problem common to confirmatory factor analysis, since when the number of input variables is large, any small deviation from the true model will cause the proposed model to fail. To judge whether a poorly fitting but plausible model was adequate, the authors employed a modified version of a reliability coefficient described by Tucker and Lewis [49]. Tucker and Lewis defined $M_m = F_m/df_m$, where F_m is the likelihood ratio statistic for model m, as defined by Jöreskog, and df_m is the number of degrees of freedom available to test the goodness of fit of model m. They argued that if $M_0 = F_0/df_0$ for model zero, having no common factors, then one may consider $E(M_0) = \alpha_m + \delta_m + \epsilon_m$ and $E(M_m) = \delta_m + \epsilon_m$, where α_m is the variance accounted for by model m, and not accounted for by model zero, δ_m is the deviation of the model from actuality and ϵ_m is the variance associated with sampling. Now $n'_m F_m$ is approximately χ^2 with degrees of freedom df_m, where $n'_m = N - 1 - (1/6)(2N + 5) - 2/3\,k$, N = the sample size, n = the number of variables in the analysis, and k is the number of latent variables in the analysis.

Now, $E(n'_m M_m) = E(n'_m F_m/df_m) = E(\chi^2_m/df_m) = 1$, which implies that $E(M_m) = 1/n'_m$. When m is the perfectly fitting model, $\delta_m = 0$ and $1/n'_m = E(M_m) = \epsilon_m$, which implies that $\epsilon_m = 1/n'_m$. So, $E(M_0) = \alpha_m + \delta_m + 1/n'_m$, and $E(M_m) = \delta_m + 1/n'_m$.

If a reliability coefficient ρ_m is defined as $\alpha_m/(\alpha_m + \delta_m)$, the amount of variance explained by the model compared to the total variance, then: $\rho_m = [E(M_0) - E(M_m)]/[E(M_0 - 1/n'_m]$.

The expected mean squares may be replaced by the observed mean squares and we have: $\rho_m = (F_0/df_0 - F_m/df_m)/(F_0/df_0 - 1/n'_m)$.

As pointed out by Martin et al [29] they did not employ the correction factor $1/n'_m$ in their statistic, but replaced it with the more conservative value of 1.

2.4.a. Univariate Analyses of Finger Ridge Counts

Total ridge count (TRC) is a univariate expression of the ridge counts on all ten fingers where each of the fingers is weighted equally in its contribution to the total. In a study of 825 males and 825 females from the British population, Holt [14] generated the following descriptive statistics. The TRC range was 0–285, with means and standard deviations, respectively, of 144.98 and 51.08 for males, and 127.23 and 52.51 for females. There was a significant difference between the means of the two sexes. Correlations between total counts on the right and left hands were .94 ± .01 for 254 males and .93 ± .01 for 240 females. After the data were corrected for mean sex differences in TRC, the following correlations were obtained: husband-wife, .05 ± .08, mother-offspring, .49 ± .04, father-offspring, .50 ± .04, midparent-child, .69 ± .03; intraclass correlation for full sibs, .50 ± .04; intraclass correlation for MZ twins, .95 ± .01; and intraclass correlation for DZ twins, .49 ± .08. These correlations provided strong evidence that TRC is an inherited trait. Holt [14] concluded that since the correlations are so close to the theoretical values under the assumption of strictly additive inheritance, the trait must be additive with no dominance present. Regression of TRC on the midparental values gave a strong linear relation, also evidence for the absence of dominance. There was no evidence for an inherited maternal effect since the parent-child correlations were essentially equal for fathers and mothers. This, of course, does not rule out the possibility of an environmental maternal effect which is caused by the mother but does not increase the mother-offspring correlation.

Holt pointed out that the nonnormality of the distribution of total ridge count suggests that a comparatively small number of genes have an appreciable effect on the trait. If there were a larger number of genes involved a more normal distribution would have been obtained. In addition, attempts to divide the distribution into three components, indicating one pair of alleles at a major locus did not meet with success. These findings, as well as others, were reiterated in her 1968 book "The Genetics of Dermal Ridges" [16].

In 1956/57, Holt presented descriptive statistics on the distributions of ridge counts on the individual fingers taken from the same British sample of 825 males and 825 females [14]. Frequency distributions for the males and females for the ten individual fingers, as well as means and standard deviations were given. Table 1 gives the means and standard deviations for each finger taken from her results. The digits in decreasing order of magnitude of their average counts are the thumb, fourth, fifth, third, and second fingers on both hands and in both sexes. On all fingers the males had higher ridge counts than the females, and differences in the means between males and females were significant for each finger. Mean ridge counts were higher on the right hand than the left hand for both sexes for all digits except for the third finger of the males.

To reflect the variation in ridge count between the ten fingers of an individual, Holt devised a statistic which she called S^2. If $q_1, \ldots q_{10}$ are the ten separate digital counts, and

$$Q = \sum_{i=1}^{10} q_i,$$

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then

$$S^2 = \sum_{i=1}^{10} q_i^2 - Q^2/10.$$

The values of S^2 ranged between 0 and about 1,050, indicating that this measure of variation in the ten separate finger ridge counts of individuals is highly variable. An attempt to relate TRC or Q and S^2 revealed a nonlinear relation between the two variables. Variances were small for low ridge counts, as could be expected, whereas variances for very large ridge counts up to a certain point around 250 were also small. For TRC values beyond 250, however, the value of S^2 was again large. It appears that variability is highest for intermediate values of ridge count.

In 1958, Holt published a paper containing the phenotypic correlations in individual finger ridge counts for the sample of 825 males and 825 females [15]. The correlations were highest for homologous fingers and ranged between .42 and .83 for males and .46 and .83 in females. The fourth fingers were most highly correlated with each other in both subsamples.

In a study of 441 unrelated individuals, Siervogel et al [45] found that the finger order for decreasing mean digital ridge count was the same as that reported by Holt, the thumb and then fingers, four, five, three, and two. They postulated that the hand was divided into three fields, the thumb, the last two fingers and the second and third fingers. This hypothesis, based on observations of mean individual finger ridge counts and pattern frequencies, was not tested statistically. Some of their observational findings that are of interest concern the index finger. It is the digit with the greatest print-type variation, the least bilateral symmetry and the highest proportion of arches.

Several univariate studies have been conducted to investigate alternatives to the strictly additive genetic model proposed by Holt for total ridge count. Spence et al [47] pointed out that Fisher's [10] z-transformation on two of Holt's correlations, MZ twin and parent-child, yielded values that were significantly different from their expected theoretical values. In this study they analyzed data from 533 Caucasian and 545 Japanese individuals. The trait studied was absolute finger ridge count which is calculated in the same way as TRC except that, for whorls, both counts are included. A model containing a mixture of three normal distributions fit the data significantly better than it fit a single normal

TABLE 1. Descriptive Statistics for 825 Males and 825 Females as Reported by Holt [16]

	Males		Females	
Finger	Mean	S.D.	Mean	S.D.
LT	19.76	6.25	16.50	6.49
L1	11.78	7.41	10.68	7.23
L2	12.02	6.48	10.82	6.23
L3	16.52	6.51	15.16	6.78
L4	14.10	5.38	12.36	5.95
RT	17.04	6.37	14.30	6.37
R1	11.34	7.05	9.77	7.03
R2	12.44	6.77	10.60	6.76
R3	16.29	6.52	14.71	7.13
R4	13.88	5.09	12.07	5.77

distribution. This was indicative of a possible single major locus with two alleles and no dominance. The authors concluded that proof of the existence of such a locus would require pedigree analysis and linkage studies.

Spence et al [47] analyzed total ridge count data from 100 families from the studies of Holt and included 30 male and 20 female MZ twin pairs. Hypotheses that the dominance variance is zero, the common environmental variance is zero and that both of these are zero were all rejected at the .01 level. Therefore dominance variance appears to be present for total ridge count according to this analysis.

Nance [33] fit a model for inheritance of total ridge count including components for additive, dominance, maternal and random environmental effects to data on families of 52 MZ twin pairs. The parameter estimates were significant for the additive and random environmental components and the narrow heritability was estimated at .79. Phelan et al [39] fit a series of models to data on the offspring of 111 MZ twin-pairs and found a best fitting model containing additive genetic and random environmental effects, with no evidence for a significant maternal influence. They obtained a heritability estimate of .89.

Reed et al [41] explored the possibility of maternal influences on 41 dermatoglyphic variables by comparing variances between sibships nested within male and female twin kinships. Significant maternal effects for five thumb related variables were found, affecting primarily the radial and individual thumb ridge counts. Four significant little finger variables were found affecting primarily the ulnar count. Their sample consisted of 555 offspring of 49 male twin kinships and 65 female twin kinships. Doubt was cast upon their findings for the little fingers, in that the mean square within sibships in male kinships was significantly larger than the mean square within sibships in female kinships. The authors concluded that the study provided additional evidence for maternal effects on the thumb. This was supported by parent-child regression coefficient of .60 and .63 for the left and right radial counts of the thumbs, and father-child regression coefficients of .25 and .32 for the respective left and right values.

It thus appears that ridge counts are strongly influenced by a small set of additive genes which could be influenced by a major gene. In addition, environmental effects, which occur in utero, may be present for the thumb and little finger. These effects do not appear to increase the mother-child correlation, therefore they are probably not inherited but act to effect the environment within the uterus.

2.4.b. Multivariate Studies of Ridge Count

In their introduction to a multivariate analysis of individual finger ridge counts, Roberts and Coope [42] pointed out that previous analyses of finger ridge counts are flawed in that studies of total ridge count ignored information contained in the separate fingers and studies on individual fingers ignored the information provided by their interrelationships. They concluded that a more complex analysis including information on individuals fingers and common effects would be necessary.

They chose as their method a principal components analysis on the phenotypic correlations between the twenty ulnar and radial counts of the ten individual fingers. They felt that departures from normality could be ignored for their exploratory analyses. They did not point out, however, that results obtained from the phenotypic correlations would be blurred by the effects of environment. Their four samples consisted of 800 males from rural and urban areas of southern England and 800 females also from the rural and urban areas in the same location. Eight principal components accounted for about 80% of the

total phenotypic variance in the sample. The first component which had a high correlation with TRC had positive loadings over all input variables and was considered a general genetic factor. The second factor discriminated between radial and ulnar counts and was not affected by the index finger. The third component reflected the counts on the thumbs, while the fourth represented a strong contrast between the radial and ulnar counts of the second finger. The authors concluded that their findings supported the second hypothesis of Bonnevie [5], that separate genes act to effect the ulnar and radial ridge counts of the fingers. While Bonnevie proposed one gene pair controlling this expression, these authors indicated the existence of a set of polygenes affecting the differences. They did not include the possibility of environmental effects on these differences, however. Thus, they proposed four factors influencing the development of dermal ridges, a general factor, a factor differentiating ulnar and radial counts, a factor influencing the middle digits and a factor influencing the outside digits. This last factor has the same structure as the maternal effects reported by Reed et al [41].

Parisi and DiBacco [38] analyzed data from 50 MZ and 50 DZ twin pairs to elucidate inheritance patterns of finger ridge counts. They concluded that total ridge count was an arbitrary construct, and that it was more informative to study the ridge counts individually.

Nance et al [36] employed the Bock and Vandenberg procedure to estimate a matrix of pure genetic effects, which was first subjected to a principal components factor analysis and then to a varimax rotation. The varimax rotation yielded a factor containing five of the six central digits which accounted for about 25% of the heritable variance in ridge counts and six other dermatoglyphic variables. A little finger factor accounting for 16% of the variance and a thumb factor accounting for 12.5% of the variance were also detected. Also observed was a left second finger factor accounting for 6% of the variance. With the exception of the index finger, all homologous fingers were loaded onto the same factor. These factors are in agreement with those detected by Roberts and Coope [42] for phenotypic variation.

Rostron [43] explored inheritance patterns for individual finger ridge counts taken as a ten variable multivariate trait in a manner similar to that described by Bock and Vandenberg. Instead of using twins, however, he maximized the multivariate parent-offspring regression coefficient and the multivariate intraclass correlation coefficient. For both, he conducted a preliminary factor analysis on the phenotypic correlations of the sample and found two significant factors. These factors maximized the parent-offspring regression coefficient and the intraclass correlation sufficiently well so that calculated matrices of genetic effects were nearly diagonal. From this procedure he found two significant factors affecting ridge counts for both males and females. There was one factor of general genetic effects on all fingers with the loadings on homologous fingers being nearly equal with a heritability of .97 and a second factor which differed for the male and female subsamples. For the males the heritability of this factor discriminating between the first two fingers and the last three fingers was .25, whereas the one discriminating between the thumb and the other four fingers for the females had a heritability of .62. The author expressed some concern about the precision of the second factor. One may conclude from Roston's research that there is one strong genetic factor affecting the ridge counts on all ten fingers and that the fingers do not contribute with equal weights to total ridge count, although homologous fingers have very similar weights. His division of the hand into two parts is in disagreement with Roberts and Cooper [42], Siervogel et al [45], and Nance et al [36], who all found the hand divided into three separate regions.

Iagolnitzer [18] developed the method of component pair analysis (CPA) to extend the principal components analysis procedure to twin data. He applied the methodology to ridge count data on one hand for 139 MZ and 92 DZ twin paris. CPA requires the arrangement of data into a 2p by 2m matrix, where p is the number of variables under analysis and m the number of twin pairs in the sample. Principal component analysis on the matrix gives a decomposition of the data into two orthogonal spaces, the between and within pair spaces. The within and between pair MZ and DZ analyses both revealed in each case one strong general factor influencing five fingers with the largest loadings being those for the middle fingers. A second factor primarily influenced the thumb and a third factor influenced fingers two and four with the signs of their loadings being opposite. Analysis of the difference in within pair MZ and DZ matrices which gave an estimate for genetic variances and covariances did not modify the structure of the components. The author concluded that perhaps we should analyze TRC as a weighted rather than unweighted univariate trait. He found three independent factors influencing the hand, one for the thumb, one for the index finger and one for the last three digits. While the number three is in agreement with previously cited authors, his division of the hand is a bit different from theirs.

Singh [46] investigated the possibility of dominance in the expression of ridge counts through a multivariate study of hybrid individuals and individuals from their parent populations. Five hundred Australian Europeans, 64 individuals from two aboriginal populations, and 103 part-aboriginals were studied. One significant canonical variable was found to discriminate among the four groups. The canonical variate was employed to plot the mean position of each population on a linear scale. The square of the distance measured between any of the two populations is approximately proportional to the generalized Mahalanobis D^2 statistic, and one may test the significance of D^2. He found a significant distance between the part aboriginals and the Europeans and the part aboriginals and one of the aboriginal tribes but not the other. The value is also significant for the distance between the part aboriginals actual value and expected value under the assumption of no dominance. This result is indicative of the possibility of dominance. Included in this analysis were five variables in addition to individual ridge counts, frequency of ulnar loops, radial loops, accidentals, triradius counts, and asymmetry. It is these five variables for which dominance might be acting. No attempt was made to separate them from the individual finger ridge counts.

2.5. The Half-Sib Model

A complete description of the half-sib model was presented by Nance and Corey [34]. The twin kinship is the basis of their analysis and consists of MZ twins, their spouses, and their offspring. A univariate analysis employing the half-sib model proceeds in the following manner. Each individual in a set of half-sibships is measured for the quantitative trait in question. Nested analyses of variance are performed separately on the data from offspring of male and female twins yielding six mean squares derived from the among, between and within sibship sums of squares. Each mean square has as its expectation a linear combination of variance components, which in turn have as their expectations certain genetic and environmental components of variance. Table 2 illustrates the combinations of genetic and environmental components which each of the mean squares has as its expectation. Estimates for the genetic and environmental parameters may be obtained by solving the resulting system of simultaneous linear equations. An iterative weighted least squares procedure suggested by Haymen [13] has been the one most often employed.

TABLE 2. Expected Mean Squares for Twin Kinships

Source of variation	Expected mean square	Genetic and environmental expectation
Half sibships ♂	$\sigma^2_W + b_1\sigma^2_S + b_2\,\sigma^2_H$	$\frac{1}{2}V_A + 3/4V_{AA} + V_{EW} + b_1\,(\frac{1}{4}V_A + 3/16V_{AA} + V_M) + b_2\,(\frac{1}{4}V_A + 1/16V_{AA})$
Sibships (half-sibships ♂)	$\sigma^2_W + b_3\sigma^2_S$	$\frac{1}{2}V_A + 3/4V_{AA} + V_{EW} + b_3\,(\frac{1}{4}V_A + 3/16V_{AA} + V_M)$
Individuals within sibships ♂ and ♀	σ^2_W	$\frac{1}{2}V_A + 3/4V_{AA} + V_{EW}$
Sibships (half-sibships ♀)	$\sigma^2_W + b_4\sigma^2_S$	$\frac{1}{2}V_A + 3/4V_{AA} + V_{EW} + b_4\,(\frac{1}{4}V_A + 3/16V_{AA})$
Half-sibships ♀	$\sigma^2_W + b_5\sigma^2_S + b_6\,\sigma^2_H$	$\frac{1}{2}V_A + 3/4V_{AA} + V_{EW} + b_5\,(\frac{1}{4}V_A + 3/16V_{AA}) + b_6\,(\frac{1}{4}V_A + 1/16V_{AA} + V_M)$

The equal availability of both male and female twin pairs permits the component for maternal effects to be included in these analyses.

An important feature of this design is that data are taken from normal children raised in their own homes by their biologic parents, which is not the case in studies that involve adopted children. Other than the selection for fertility, there are few biases in ascertainment through twin parents, as monozygotic twinning occurs with equal frequencies in all racial groups and is not known to be associated with fertility drugs or other environmental effects. The design permits the estimation of effects due to the interactions of genes. With other designs, epistasis and dominance have been difficult to detect.

Studies of necessary sample size and MZ twinning rates indicate the feasibility of half-sib analyses. For studies of univariate traits on the offspring of MZ twins, Kang et al [23] found that the variance of the estimates of additive genetic effects begin to stabilize with samples of between 100 and 200 kinships for heritabilities greater than or equal to .2. Nance and Corey [34] pointed out that the incidence of MZ twinning is .004 for all racial groups, so that a reasonable number of families may be studied in a large population center.

Several extensions of the half-sib model have been proposed. Corey and Nance [6] extended the half-sib model to include the grandchildren of MZ twins. This design facilitates the investigation of the sources of maternal effects. Winter et al [52] and Corey et al [7] extended the model to resolve the contribution of genetic and environmental effects to qualitative traits. Analysis of traits that are X-linked were discussed in the 1976 paper by Nance and Corey [34].

Criticisms of the half-sib design were given by Chakraborty and Morton in the discussion following the paper of Nance et al [35]. Chakraborty expressed concern about the model-fitting strategy, by which chi-square statistics and their associated p values were compared for a set of models which fit, in order to find the best fitting model. He pointed out that the best χ^2 value may have occurred by chance. He also was concerned about the pattern by which the standard errors of component estimates were larger for models which fit than for those that didn't. Morton asserted that the assumptions of normality, homoscedasticity, and large sample size were not met in the reported half-sib studies. Homoscedasticity was violated particularly in analyses of traits that varied with age. He concluded his remarks with a criticism asserting that individuals who are MZ twins are unusual and that inferences drawn from the offspring of these individuals should not be generalized to

the population at large. Eaves et al [8], on the other hand, found the half-sib model as an attractive alternative to the MZ-DZ twin analysis. They concluded that the design could be used to detect the effects of maternal genotype without the confounding effects of parity and environment.

3. MATERIALS AND METHODS

3.1. The Sample

The sampling unit for this analysis of data on individual finger ridge counts consisted of the offspring of a pair of adult monozygotic twins (MZ kinship). If either twin had more than one spouse, only one full sibship, usually that full sibship for which there was the most complete information, was included in the analysis. In addition, kinships were included in the sample only if they contained at least one individual in each of the full sibships nested within them.

Kinships were ascertained through personal referral by previous participants and through individuals associated with "mothers of twins" clubs. While units in the sample are not independent, this should be of no great consequence for a trait such as ridge count. Data from kinships were collected at Indiana University during the years 1970 through 1975 under the supervision of Dr. Walter E. Nance. Additional kinships were studied at the Medical College of Virginia between 1975 and 1981. All members of the study were classified as white.

Zygosity of the twins was decided by complete genotyping for a minimum of seven red cell antigens (Hp, PGM, Ap, Hb, G6PD, 6PGD, Cf, LDH) and three serum proteins (Hp, PGM, AP). A difference in the phenotypes for any one of these systems implied dizygosity. If the twins were concordant for all test systems, a relative probability of monozygosity versus dizygosity was calculated from the nine phenotypes. In all instances the probability of monozygosity was greater than 0.99.

The sample was composed of 48 kinships consisting of the 222 offspring of male MZ twins and 59 kinships consisting of the 287 offspring of female MZ twins.

3.2. Dermatoglyphic Data

Rolled finger prints were taken by the inkless method of the Faurot Company. Digits were coated with a solution of resensitizing fluid, which is sold commercially by the company, and then each finger was rolled across hand and palm print paper, also marketed by Faurot. The prints were taken and analyzed by experienced technicians working in the twin clinic, who performed the task consistently. Ridge counts were determined according to the procedure described in the introductory chapter.

3.3. Statistical Analyses

3.3.a. Preliminary Computations. The mean, standard deviation, skewness, and kurtosis were calculated for ridge counts on each of the ten fingers for the total sample and the subsamples of males and females using the Univariate procedure of the Statistical Analysis System [44] package. Histograms were generated for each of these distributions using the SAS graphics package. These statistics were used to standardize the individual finger ridge counts in order to adjust for differences due to sex. For within sex finger categories, the mean for each finger was subtracted from each observation and the difference divided by the associated standard deviation. Thus ten different adjustments were made for each individual, one for each finger. Hence, the entire sample of finger

ridge counts was standardized to a mean of zero and a standard deviation of one. These data became input for all subsequent analyses.

Multivariate nested analyses of variance were conducted separately on the offspring of male twins (male kinships), the offspring of female twins (female kinships), and the combined sample of offspring, using the Nested procedure of the Statistical Analysis System. The linear model upon which these analyses were based is as follows

$$R_{ijk} = \mu + H_i + S_j(H_i) + I_{ijk}$$
$$1 \leqslant i \leqslant n$$
$$j = 1,2$$
$$1 \leqslant k \leqslant n_{ij}$$

where R_{ijk} is the vector of ten individual ridge counts for the kth individual in the jth sibship in the ith kinship, μ is the vector of mean ridge counts for the total population, H_i is the vector of deviations from μ of the mean ridge counts in kinship i, $S_j(H_i)$ is the vector of deviations from the mean ridge counts in kinship i of the mean ridge counts in sibship j nested within kinship i, I_{ijk} is the vector of deviations of the ridge counts of individual k from the mean ridge counts of sibship j within kinship i, n is the number of twin kinships, and n_{ij} is the number of offspring in sibship j within kinship i.

Output of the Nested procedure included the mean squares for each of the ten input variables, as well as the mean cross products for their pairwise combinations. They were given for each level of effects in the linear model. These were assembled into five matrices corresponding to the five mean squares of a univariate analysis. Mean sums of squares and cross products for the among male kinship effect for the 10 ridge counts yielded a symmetric 10 × 10 matrix in which there were 55 unique statistics. An analogous matrix was constructed for the among female kinship effects, and two other matrices were obtained for the between male sibship and between female sibship effects respectively. A fifth matrix was determined from the error effects of the total sample. In all, there were 275 unique statistics with which to estimate parameters and test hypotheses.

3.3.b. The Bock and Vandenberg Analysis. Input for the Bock and Vandenberg [see 4] analysis was a single matrix obtained by conducting a nested analysis of variance on a subset of balanced male kinships. The balance was achieved by omitting from the data set all kinships which did not have at least two offspring in each of the two full sibships within it. In addition, kinships with greater than two individuals in a full sibship were truncated so that only the first two individuals born to the twin in that sibship were included in the analysis. Thus, a set of balanced kinships was generated, containing two offspring in each full sibship.

Statistics on the balanced kinships were necessary so that a direct estimate of additive genetic effects could be obtained. For this set of kinships,

$$\text{E(MSA)} = \text{E(Mean square among male kinships)} = 4\sigma_A^2 + 2\sigma_B^2 + \sigma_E^2$$
$$\text{E(MSB)} = \text{E(Mean square between male kinships)} = 2\sigma_B^2 + \sigma_E^2$$

where σ_A^2, σ_B^2, and σ_E^2 are the among, between, and error variance components from the nested analysis of variance. Thus, it was possible to estimate $4\sigma_A^2$ from the product $(\text{MSA})(\text{MSB})^{-1}$. Since $E(\sigma_A^2)$ is $\frac{1}{4}V_A$ for male kinships, $E(4\sigma_A^2)$ is V_A. Hence $(\text{MSA})(\text{MSB})^{-1}$ is an estimate of the matrix of additive genetic effects V_A. This product matrix was obtained from the output of the General Linear Models procedure

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of the Statistical Analysis System, for which the nested model (1) was invoked. The output also included the eigenvalues and eigenvectors of the product matrix.

The matrix of genetic effects was reconstructed according to the method of Bock and Vandenberg [4] in order to ensure it was at least positive semidefinite. That is, V_A was estimated as $(X^{-1})'L(X^{-1})$, where X was the matrix of eigenvectors of $(MSA)(MSB)^{-1}$ and L the diagonal matrix of the adjusted eigenvalues. Eigenvalues were adjusted by decreasing each by 1. If this reduction resulted in a value less than 1, the eigenvalue was set equal to 0. This procedure provided a matrix estimate of genetic effects which was appropriate for factor analysis. In order to detect the sources of heritable variation, this matrix was subjected to a principal component analysis.

3.3.c. Confirmatory Factor Analysis. The LISREL IV program, written by Karl Jöreskog and Dag Sörbom [22], was employed to estimate genetic and environmental effects and test multivariate models for inheritance patterns of individual finger ridge counts. The authors describe LISREL as a general computer program for estimating the unknown coefficients in a set of linear structural equations. It may be adapted for the procedure of confirmatory factor analysis, however, and we have done so for these analyses.

The general LISREL model consists of two parts: the measurement model and the structural equation model. The structural equation model $\beta\eta = \Gamma\xi + \zeta$ specifies causal relations among latent variables, while the measurement model $y = \Lambda_y\eta + \epsilon$, $x = \Lambda_x\xi + \delta$ specifies how the latent variables are measured in terms of the observed variables. Here η and ξ are vectors of latent variables, while x and y are vectors of observed variables. ϵ and δ are vectors of measurement errors in x and y respectively. β and Γ are coefficient matrices while ζ is a vector of residuals. Λ_y and Λ_x are regression matrices of y on η and x on ξ respectively. It is assumed that ϵ and δ are uncorrelated with η, ζ, and ξ but may be correlated among themselves, and that $E(\eta) = 0$, $E(\zeta') = 0$ and $E(\xi) = 0$.

In this model, the variance-covariance matrix of $z = (y', x')$ is

$$\Sigma = \begin{matrix} \Lambda_y(\beta^{-1}\Gamma\Phi\Gamma'\beta'^{-1} + \beta^{-1}\Psi\beta'^{-1})\Lambda'_y + \Theta_\epsilon & \Lambda_y\beta^{-1}\Gamma\Phi\Lambda'_x \\ \Lambda_x\Phi\Gamma'\beta'^{-1}\Lambda'_y & \Lambda_x\Phi\Lambda'_x + \Theta_\delta \end{matrix}$$

where ϕ is the covariance matrix of ξ, ψ is the covariance matrix of ζ, and Φ_ϵ and Φ_δ are the covariance matrices of ϵ and δ, respectively.

For the purposes of this study, only one vector of latent variables η and one vector of observed variables y have been proposed. The simplified model is the subset of LISREL which is appropriate for confirmatory factor analysis. It is as follows, $\beta\eta = \xi$, $y = \Lambda_y\eta + \epsilon$ with variance-covariance matrix $\Sigma = \Lambda_y(\beta^{-1}\psi\beta'^{-1})\Lambda'_y + \Theta_\epsilon$

We have used this portion of the LISREL model to estimate genetic and environmental effects and to test multivariate models for inheritance patterns of individual finger ridge counts. The same procedures may be invoked to test proposed inheritance patterns for other sets of genetically related metric traits as well.

In the LISREL model, each genetic and environmental effect is represented by at least one η factor. Loadings on the factors for each of the input variables, in this case the standardized individual finger ridge counts, may be fixed at certain values, constrained to be equal to other parameters, or freed to be estimated by the method of maximum likelihood. These loadings are contained in the Λ_y matrix. The matrix ψ contains the covariances between these factors, and Θ_ϵ is a matrix of variances and covariances which

cannot be accounted for by the factors in η. The β matrix contains a set of weights which we have employed for two purposes; first, for the factors associated with a given input matrix, the weights were used to differentiate between the genetic and environmental effects specified by the expected values of the genetic model employed; and second, the weights which differed between matrices represented differences in the expectations arising from unequal sibship and kinship sizes. An annotated sample LISREL program, employed in the analysis of ridge count data on the offspring of MZ twins, is given in Appendix A.

Once the data were input to the program and the proposed model of inheritance specified, estimates of the freed and constrained factor loadings in Λ_y and variances and covariances in ψ and Θ_ϵ were obtained by the method of maximum likelihood. The likelihood function was derived for the program under the assumption of multivariate normality. A linear function of it,

$$F = \sum_{g=1}^{m} \frac{N_g}{N} [\log|\Sigma^g| + \mathrm{tr}(S^g(\Sigma^g)^{-1})\log|S^g| - p]$$

where N_g is the number of observations in group g and

$$N = \sum_{g=1}^{m} N_g$$

is the expression which is actually minimized. F is a multiple of the log likelihood ratio statistic for the proposed model compared to the perfectly fitting theoretical model. Jöreskog and Sörbom [22] have employed a modified version of the 1963 Fletcher-Powell [11] algorithm to minimize F. This procedure is discussed in detail in 2.3.

Output from a LISREL analysis includes estimates of freed and constrained parameters, as well as their standard errors and associated t vaues. A chi square goodness of fit statistic is also given which may help one to decide whether a proposed model is appropriate. This statistic is defined as the minimum value of F with degrees of freedom $d = (\frac{1}{2})p(p + 1)G - t$, where G is the number of input matrices, p is the number of input variables, and t is the total number of independent parameters estimated in all groups.

There are several methods which are useful in determining the appropriateness of a proposed model that are available to the LISREL user. First, the chi squre value and its associated p value may be used to reject models when the p value falls below a certain criterion. This procedure is most often used to decide between alternative models. A second method, if the model does not fit, involves the examination of its chi square value in comparison to one for a model which is more restrictive. One can use the difference in chi square values with respect to the difference in degrees of freedom to decide whether additions to a model are useful. If the difference in chi squares is significant for the difference in degrees of freedom, one usually assumes the addition of parameters or factors to be appropriate. A third option used in deciding upon a model is to employ the statistic proposed by Tucker and Lewis [49] to examine the percentage of unexplained variation accounted for by the model. This statistic has been modified by Eaves et al [9] for a similar analysis on MZ and DZ twins. To calculate this statistic, one estimates the chi square value of an "absurd" model, such as one which contains only random

environmental effects and compares that with the chi square statistic for the model under question according to the following formula:

$$T = \left[\frac{{\chi_0}^2}{df_0} - \frac{{\chi_1}^2}{df_1}\right] \qquad \left[\frac{{\chi_0}^2}{df_0} - 1\right],$$

where χ_0^2 is the statistic under the "absurd" model and χ_1^2 is the statistic under the proposed model and df_o and df_1 are their respective degrees of freedom. T gives the percent of the variance unexplained by the "absurd" model that can be explained by the proposed model. One may of course modify this so that the "absurd" model is any one which fits more poorly and is more restrictive than the model under analysis. All three procedures were used in deciding which models best explained the inheritance patterns seen for individual finger ridge counts.

4. RESULTS AND DISCUSSION

4.1. Descriptive Statistics

The mean, standard deviation, skewness, kurtosis, and sample size for the individual fingers, as well as total ridge count of the total sample, are given in Table 3. The statistics have also been calculated for the subsample of males (Table 4), and the subsample of females (Table 5). In this study, means of the males for the individual fingers are in every case smaller than those reported by Holt [15] for a sample of 825 males taken from the British population, except for the right thumb. As one would expect, however, the order of the fingers sorted according to descending values of ridge count is constant across hands, sexes and populations. The fingers in decreasing order are: thumb, fourth finger, fifth finger, third finger, second finger. As with Holt's sample, the female counts are smaller than the male counts; however, in the present sample the average ridge count is higher on the fourth finger of the right hand for females than it is for males. These sex differences necessitated the standardization of the ridge counts, a procedure described in Materials and Methods.

Skewness and kurtosis values for the standardized ridge counts over the total sample, shown in Table 6, reveal significant deviations from normality, especially for the thumb. Figure 1a–j are histograms of the sample values of these standardized counts. These

TABLE 3. Descriptive Statistics: Ridge Counts of the Total Sample

Finger	n	Mean	Standard deviation	Skewness	Kurtosis
LT	519	15.13	6.11	−.49**	.30
L1	518	10.38	6.29	.15	−.12
L2	518	10.91	5.83	−.28**	−.43*
L3	518	14.67	5.70	−.20*	.17
L4	517	12.71	5.09	−.21*	.22
RT	516	17.14	5.59	−.72**	1.21**
R1	517	10.91	6.72	.04	.46**
R2	519	11.10	5.33	−.28**	−.39*
R3	518	14.57	5.86	−.10	−.01
R4	519	12.88	5.07	−.16	−.52*
TRC	509	130.68	44.59	−.28**	−.12

* = $p < .1$.
** = $p < .02$.

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TABLE 4. Descriptive Statistics: Ridge Counts of the Subsample of Males

Finger	n	Mean	Standard deviation	Skewness	Kurtosis
LT	268	16.21	5.69	−.53**	.56*
L1	267	10.47	6.50	.17	−.11
L2	267	11.38	5.84	−.33*	−.30
L3	266	14.98	5.56	−.11	.35
L4	266	13.32	4.99	−.11	−.05
RT	266	17.97	4.99	−.61**	.94**
R1	266	11.00	6.96	.05	.54*
R2	267	11.24	5.35	−.23	−.34
R3	266	14.50	5.73	−.12	−.25
R4	267	13.52	4.70	−.15	−.28
TRC	263	134.98	44.01	−.15	−.30

* = p < .1.
** = p < .02.

TABLE 5. Descriptive Statistics: Ridge Counts of the Subsample of Females

Finger	n	Mean	Standard deviation	Skewness	Kurtosis
LT	251	13.99	6.34	−.40**	.11
L1	251	10.28	6.07	.12	−.15
L2	251	10.41	5.79	−.23	−.52*
L3	251	14.33	5.84	−.26*	−.02
L4	251	12.06	5.12	−.30*	−.48
RT	250	16.25	6.06	−.68**	1.03**
R1	251	10.80	6.47	0.01	−.38
R2	252	10.95	5.31	−.33*	−.45
R3	252	14.65	6.00	−.09	.21
R4	252	12.21	5.35	−.08	−.74*
TRC	246	126.09	44.83	−.42**	−.04

* = p < .01.
** = p < .02.

TABLE 6. Descriptive Statistics: Ridge Counts of Sex-Adjusted Total Sample

Finger	Skewness	Kurtosis
LT	−.47**	.33
L1	.14	−.14
L2	−.28**	−.42*
L3	−.18*	.16
L4	−.20*	−.26
RT	−.64**	.96**
R1	.04	−.47*
R2	−.28**	−.40*
R3	.11	−.04
R4	−.12	−.51*

* = p < .1.
** = p < .02.

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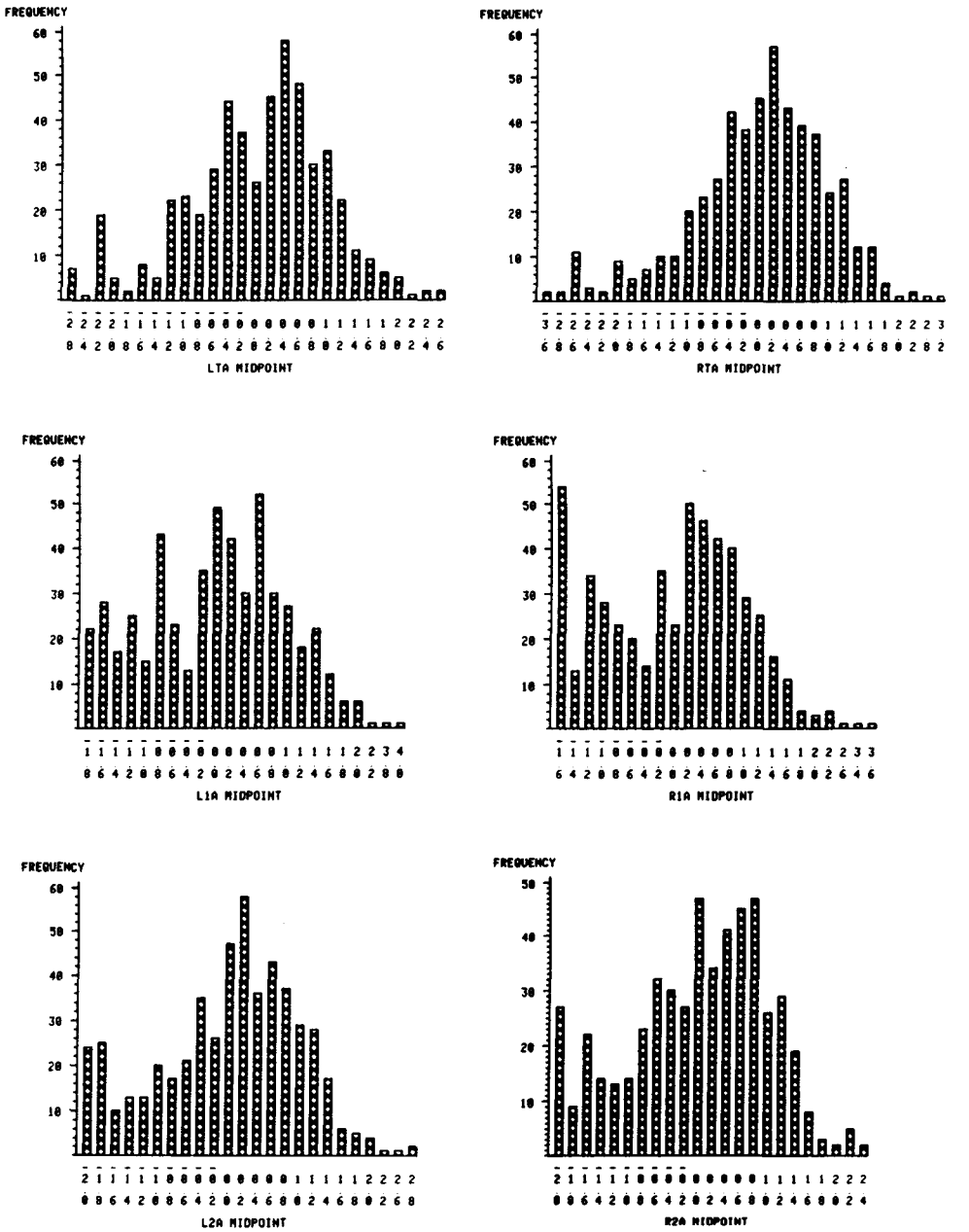

Fig. 1. (a–f) Histograms of sex-adjusted finger ridge counts for thumbs, index, and third fingers of left and right hands.

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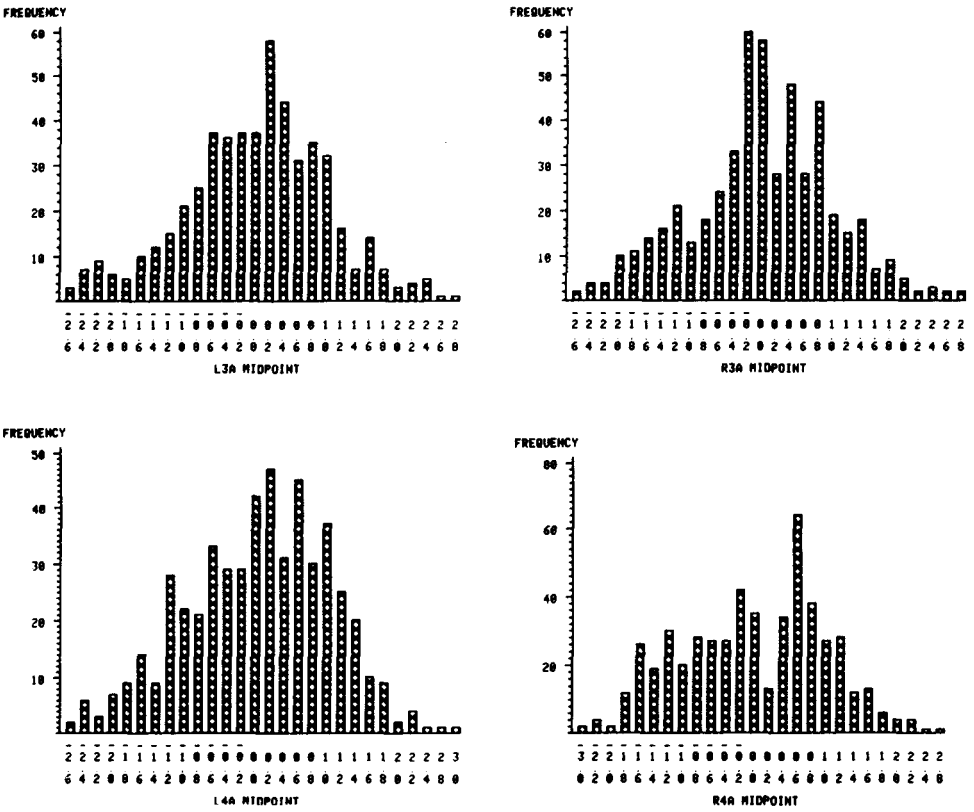

Fig. 1. (g–j) Histograms of sex-adjusted finger ridge counts for fourth and fifth fingers of left and right hands.

histograms present evidence for the nonnormality of the marginal distributions of the counts on all ten fingers, and hence, evidence for nonnormality of the multivariate distribution of the ten individual finger ridge counts. No transformations of the marginal distributions were performed, however, since this procedure does not ensure multivariate normality. It was assumed that the procedures employed in the analyses are robust against these deviations. Further investigations of problems of nonnormality are warranted, however.

Mean sums of squares and cross products for each level of effects in the nested analyses of variance for all ten standardized individual finger ridge counts are given in Tables 7–11. Included with these data are the weighting values ($b_1 - b_6$) due to unequal family sizes. These were used as coefficients in the linear combinations of variance components, which formed the expected values of the five mean sums of squares and cross products matrices (see Table 2).

4.2. The Bock and Vandenberg Analysis

Data from 30 balanced male kinships were analyzed to obtain estimates of a matrix of additive genetic effects according to the procedure of Bock and Vandenberg [4]. Eigenvalues and eigenvectors of $(MSA)(MSB)^{-1}$ were combined to estimate a matrix of

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*TABLE 7. Mean Sums of Squares and Cross Products Matrix From the Multivariate Nested ANOVA (Among Male Kinships)**

	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	2.040									
L1	1.106	1.643								
L2	1.358	1.436	2.077							
L3	1.234	1.566	1.754	2.291						
L4	1.057	1.357	1.309	1.717	2.158					
RT	1.777	1.044	1.434	1.205	1.172	2.204				
R1	0.926	1.398	1.367	1.450	1.192	1.068	1.539			
R2	1.169	1.447	1.878	1.713	1.140	1.224	1.398	2.191		
R3	0.890	1.272	1.438	1.775	1.400	1.014	1.247	1.431	1.698	
R4	0.669	1.094	1.171	1.307	1.590	0.946	1.115	1.181	1.168	1.788

*$b_1 = 2.567$, $b_2 = 4.790$, df = 47.

*TABLE 8. Mean Sums of Squares and Cross Products Matrix From the Multivariate Nested ANOVA (Between Sibships Within Male Kinships)**

	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	1.319									
L1	0.727	1.420								
L2	0.722	0.860	1.170							
L3	0.642	0.757	0.789	1.042						
L4	0.800	0.651	0.818	0.817	1.294					
RT	1.152	0.814	0.807	0.733	0.805	1.432				
R1	0.630	0.980	0.675	0.587	0.533	0.669	1.109			
R2	0.548	0.812	0.705	0.587	0.587	0.695	0.677	0.884		
R3	0.658	0.540	0.756	0.679	0.792	0.808	0.594	0.549	1.078	
R4	0.886	0.860	0.893	0.771	1.158	0.990	0.705	0.674	0.928	1.491

*$b_3 = 2.234$, df = 48.

*TABLE 9. Mean Sums of Squares and Cross Products Matrix From the Multivariate Nested ANOVA (Within Sibships)**

	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	0.581									
L1	0.223	0.553								
L2	0.190	0.266	0.642							
L3	0.204	0.195	0.269	0.537						
L4	0.197	0.215	0.215	0.282	0.571					
RT	0.337	0.182	0.200	0.246	0.158	0.564				
R1	0.165	0.293	0.320	0.267	0.233	0.198	0.646			
R2	0.196	0.296	0.363	0.281	0.223	0.214	0.323	0.647		
R3	0.208	0.274	0.291	0.396	0.345	0.254	0.287	0.351	0.703	
R4	0.247	0.247	0.210	0.291	0.371	0.251	0.194	0.214	0.378	0.621

*df = 307.

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*TABLE 10. Mean Sums of Squares and Cross Products Matrix From the Multivariate Nested ANOVA (Between Sibships Within Female Kinships)**

	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	0.912									
L1	0.542	1.072								
L2	0.291	0.413	0.790							
L3	0.363	0.579	0.669	0.992						
L4	0.384	0.496	0.377	0.570	0.823					
RT	0.458	0.417	0.279	0.386	0.285	0.688				
R1	0.685	0.946	0.605	0.781	0.513	0.508	1.391			
R2	0.341	0.496	0.632	0.667	0.330	0.280	0.776	1.022		
R3	0.286	0.515	0.523	0.776	0.468	0.245	0.717	0.591	0.911	
R4	0.346	0.477	0.235	0.429	0.593	0.258	0.511	0.215	0.368	.773

*$b_4 = 2.79$, df = 59.

*TABLE 11. Mean Sums of Squares and Cross Products Matrix From the Multivariate Nested ANOVA (Among Female Kinships)**

	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	2.176									
L1	1.217	2.359								
L2	1.199	1.628	1.962							
L3	1.287	1.880	1.586	2.276						
L4	1.272	1.449	1.288	1.739	2.134					
RT	1.807	1.244	1.034	1.194	1.418	2.365				
R1	1.140	1.890	1.507	1.651	1.287	1.174	1.970			
R2	1.223	1.697	1.583	1.601	1.435	1.316	1.438	1.921		
R3	1.168	1.596	1.347	1.841	1.602	1.197	1.377	1.435	1.922	
R4	1.015	1.400	1.033	1.634	1.826	1.321	1.208	1.425	1.598	2.172

*$b_5 = 2.626$, $b_6 = 4.898$, df = 58.

additive genetic effects. That is $V_A = (X^{-1})'LX^{-1}$, where X is the matrix of eigenvectors and L is the matrix of adjusted eigenvalues of $(MSA)(MSB)^{-1}$. V_A written as a correlation matrix is given in Table 12. Results of a principal axis factor analysis of this matrix of genetic effects are given in Table 13.

Three significant additive genetic factors have been detected by this method. The first accounts for approximately 75% of the variance in individual finger ridge counts and has a strong positive effect on all ten fingers. It influences the three middle fingers of both hands most strongly and has a lesser effect on the thumb and little finger. The second and third orthogonal factors account for approximately 16 and 6% of the variance in ridge counts, respectively. The second factor primarily explains the variation in the thumbs and little fingers with the thumbs loading on the factor with positive weights and the little fingers loading with negative weights. Thus the genetic factor which increases ridge counts on the thumbs decreases the counts on the little fingers. The third orthogonal factor exerts the strongest influence on the right thumb and may imply that there are different genes which influence the ridge counts on the two thumbs.

The findings of this analysis are consistent with those of Nance et al [36] in which a varimax rotation of their Bock and Vandenberg estimate of genetic effects for individual finger ridge counts revealed four independent factors, one for the thumbs, one for the

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TABLE 12. Estimated Matrix of Genetic Correlations Between Individual Finger Ridge Counts From the Bock and Vandenberg Analysis

	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	1.0									
L1	.68	1.0								
L2	.88	.84	1.0							
L3	.57	.95	.99	1.0						
L4	.33	.88	.53	.80	1.0					
RT	.84	.48	.77	.40	.27	1.0				
R1	.69	.85	.93	.89	.71	.73	1.0			
R2	.82	.84	.95	.88	.50	.57	.82	1.0		
R3	.62	.91	.87	.98	.68	.38	.84	.94	1.0	
R4	.10	.67	.52	.79	.79	.21	.78	.46	.69	1.0

TABLE 13. Results of Principal Axis Factor Analysis of the Estimated Matrix of Genetic Effects

	Factor[a]		
Finger	1	2	3
LT	.758	.624	.037
L1	.948	−.147	−.057
L2	.968	.259	−.061
L3	.972	−.227	−.153
L4	.754	−.495	.216
RT	.643	.613	.463
R1	.956	−.003	.232
R2	.918	.197	−.320
R3	.935	−.144	−.301
R4	.701	−.610	.263

[a]Portion of variance explained by each factor: 1, 74.6%; 2, 15.8%; 3, 6.1%.

fifth fingers, and one for all middle fingers except the left index finger, which loaded onto its own factor. Bilateral symmetry and opposition of the thumb and fifth finger appear to be the strongest inferences which can be drawn when results of both of these analyses considered simultaneously.

4.3. Confirming Factor Analysis

Using the LISREL IV computer program, a series of increasingly more complex models constructed to explain the inheritance patterns of individual finger ridge counts were fit to the multivariate half-sib data. To begin, a simple random environmental model was proposed in which the variances and covariances in individual finger ridge counts could be accounted for strictly by the separate effects of environment on each finger. By excluding a common factor for all fingers, the assumption was made that no significant covariances between the adjusted ridge counts of the fingers were present. A pictorial representation of this model is given in Figure 2. The individual environmental variances, located in the diagonal matrix, Θ_ϵ, of the LISREL model are indicated by arrows. Estimates of these variances, as well as their associated t values, the same number for each estimate, are also given. As one would expect with input variables of standard

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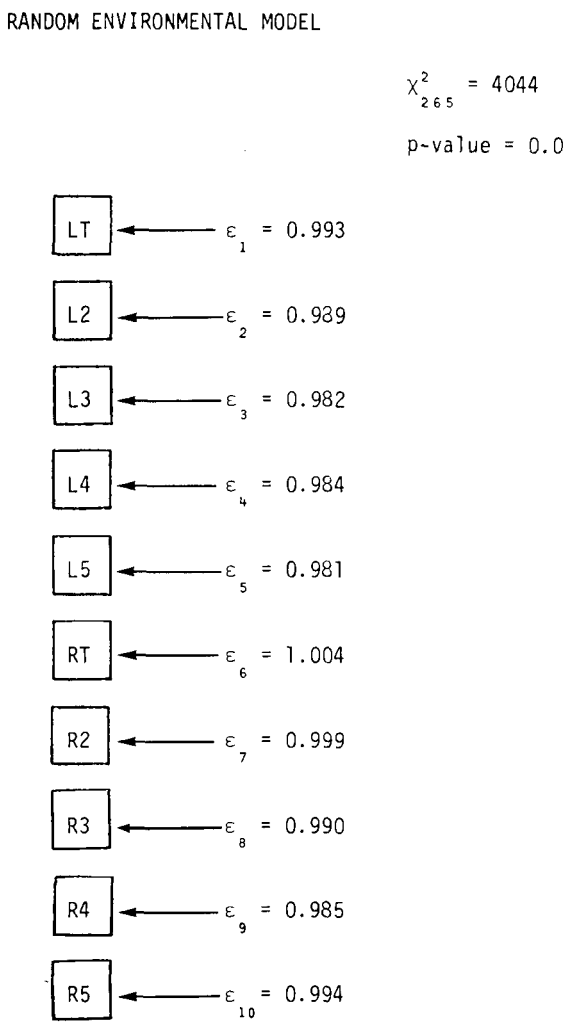

Fig. 2. Pictorial representation and parameter estimates for random environmental model for ridge count determination.

deviation one, the estimates of the individual variances are also approximatley one. Further, the fit of the model is predictably quite poor, with $\chi^2_{265} = 4{,}044$.

A more complex model, designed to test Holt's original hypothesis that total digital ridge count is a classic example of a polygenic trait, was then proposed. Under this model, one set of additive genes contributing to each of the ridge counts equally, as well as random environmental influences, also affecting all of the fingers equally, were postulated to represent total ridge count. Since total ridge count is the sum of individual ridge counts, all fingers have been hypothesized to contribute to that total with equal weights. This was accomplished in the LISREL model by constraining all of the loadings on the additive factor in the Λ_y matrix to be equal. The equal environmental impacts were represented by a similar constraint on all elements of Θ_ϵ.

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A diagrammatic representation of the model is given in Figure 3. Also contained in Figure 3 is the parameter estimate for the factor loading λ and the environmental variance Θ_ϵ, as well as the associated t values. One may use these estimates to calculate a heritability value for ridge count which is the same for each finger. This value $H^2 = \lambda^2/(\lambda^2 + \Theta_\epsilon) = .732^2/(.732^2 + .439) = .55$.

On the surface this estimate of heritability appears to be surprisingly low when compared to others reported for TRC, however there is a reasonable explanation for this discrepancy. If the heritability of the ridge count on each individual finger is .55, we may attribute as much as 45% of the variance in ridge count on each finger to the impact of environment. Environment will sometimes cause a ridge count to increase beyond the value attributable to genetic effects and sometimes cause it to decrease. When the sum for

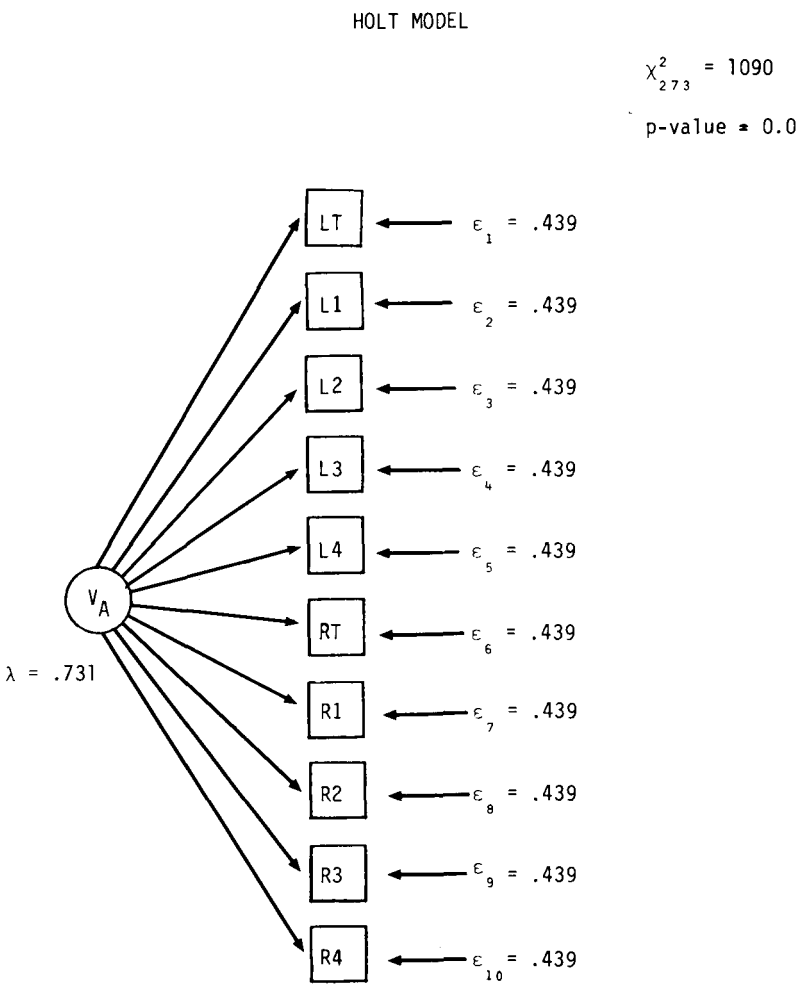

Fig. 3. Pictorial representation and parameter estimates for Holt model for ridge count determination.

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total ridge count is taken, these positive and negative environmental contributions will tend to cancel each other, making total ridge count appear to be a highly heritable trait.

The chi square goodness of fit statistic for the Holt model is 1,090 with 273 degrees of freedom. The associated p value, which is less than .0001, indicates a poor fit. In comparison with the random environmental model, however, the addition of the common genetic factor markedly improves the goodness of fit. There is a chi square difference of 2,954 for 8 degrees of freedom. We may, therefore, conclude that the additive factor, while it does not explain all the covariation between fingers, is quite necessary for the model.

If we apply the statistic developed by Tucker and Lewis [49] for calculating the proportion of variation in ridge count unexplained by the random environmental model and explained by the Holt model, the percentage is 79%. Thus, the addition of one additive genetic factor accounts for a great deal of the covariation between individual finger ridge counts. The Holt model is quite useful for explaining ridge counts, but in the presence of newer statistical methods can easily be improved upon.

Two alternatives presented themselves for refining the Holt model for inheritance patterns of individual finger ridge counts: additional factors which represent effects such as dominance, epistasis, or the maternal environment, could be added to the model; or the effects associated wth additive genetic variance could be refined and built upon. The latter approach was chosen, and, through reasoning and trial and error, the model illustrated in Figure 4 was derived. The model includes eight additive factors; one for each pair of homologous fingers, one for each side of the body, and, as with the Holt model, one general additive genetic factor. Constraining the loadings from homologous fingers on both the general factor V_{AG} and the individual finger factors V_{A1}–V_{A5} to be equal gave an improved fit over the same model with unconstrained parameters. Loading on the laterality factors V_{AL} and V_{AR} were not constrained in any way, however, since these parameter estimates will reflect asymmetry in ridge count development.

Table 14 gives the loadings on these eight factors for the ten fingers, as well as their associated t values in addition to environmental variances and their associated t values. The heritabilities of individual finger ridge counts derived from the parameter estimates for this model are also included in Table 14. These heritabilities are higher than those estimated from the multivariate Holt model, however, and in nine out of ten cases are considerably smaller than the univariate heritability estimate for total ridge count.

The poor fit is indicated by a chi square value of 360 with 245 degrees of freedom and a p value less than .0001. The difference in chi square of 730 between the full genetic model and the Holt model for the number of degrees of freedom, 28, implies a significant improvement in fit, however. In addition, the Tucker and Lewis [49] statistic indicates that the model explains 96.7% of the variance unexplained by the random environmental model and 84.3% of the variance unexplained by the Holt model. Thus, including finger and laterality additive genetic effects and constraining the loadings of the general and individual factors to be equal for homologous fingers, provides a biologically plausible, significant improvement over the model implied in Holt's analyses.

The next step in the analytic procedure involved building upon the previous model by adding the appropriate factors for other genetic and environmental effects. One genetic factor was added to account for epistatic effects, which reflected the interaction of genes located at separate loci and which were common to the expression of ridge counts on all fingers. Also included in this model was a general factor for random environment, which represents the unique effects of the uterine environment during gestation and mirrors the

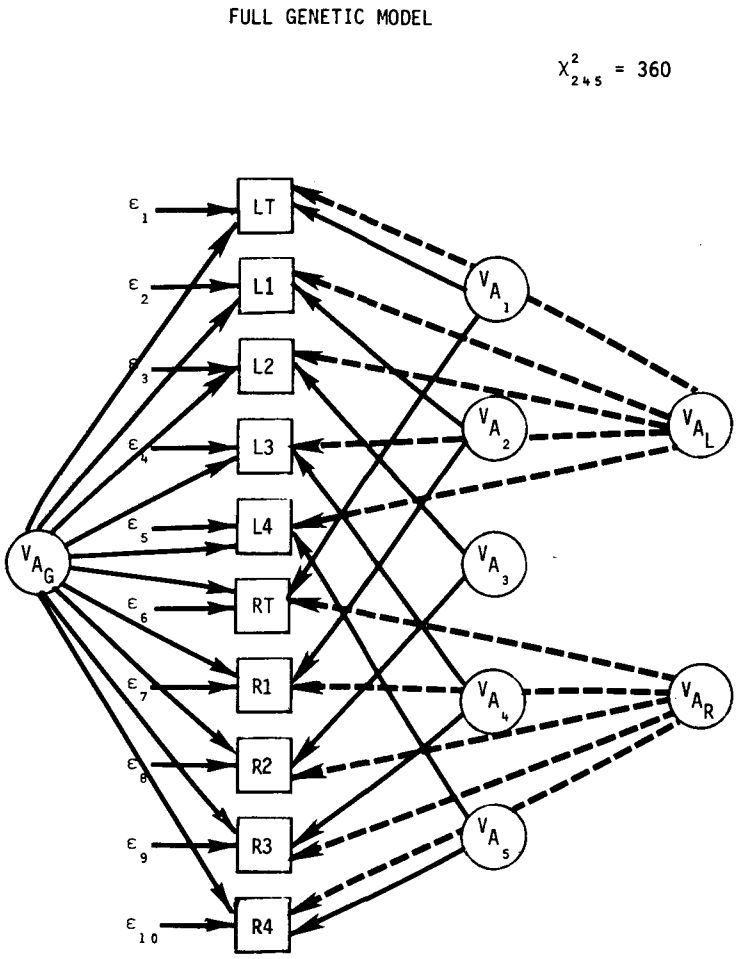

Fig. 4. Pictorial representation of full additive model for ridge count determination.

impact of the environment provided uniquely by the mother during each pregnancy. A factor for maternal effects which reflects the impact of the uterine environment common to all pregnancies of an individual was taken into account by the inclusion of a factor for maternal effects. Table 15 presents the chi square values, degrees of freedom, and P values for models including each of these factors individually, their pairwise combinations, and all three of the effects.

The addition of single factors for epistasis and environment each significantly improved the fit of the full additive model. For 10 degrees of freedom the epistasis factor decreased the chi square value by 61 while the environmental factor decreased the chi square value by 57. The addition of the single factor for maternal effects decreased the chi square value

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TABLE 14. Factor Loadings and Random Environmental Variances for the Full Additive Model (With Associated t Values)

Finger	Factor									
	V_{AG}	V_{AL}	V_{AR}	V_{AT}	V_{A1}	V_{A2}	V_{A3}	V_{A4}	θ_e	h^2
LT	.588	.018		.604					.263	.73
	(14.9)	(.27)		(19.8)					(9.6)	
L1	.748	−.030			.367				.270	.72
	(20.7)	(−.50)			(10.1)				(10.5)	
L2	.751	.103				.346			.292	.81
	(21.1)	(1.79)				(9.6)			(11.2)	
L3	.799	.168					.304		.184	.80
	(23.0)	(3.02)					(8.3)		(8.5)	
L4	.687	.291						.516	.161	.84
	(18.2)	(4.28)						(17.5)	(4.8)	
RT	.588		.381	.604					.149	.97
	(14.9)		(6.14)	(19.8)					(3.8)	
R1	.748		.029		.367				.308	.69
	(20.7)		(.59)		(10.1)				(11.5)	
R2	.751		.066			.346			.283	.71
	(21.1)		(1.33)			(9.6)			(11.2)	
R3	.799		.136				.304		2.64	.74
	(23.0)		(2.78)				(8.3)		(11.3)	
R4	.687		.189					.516	.223	.78
	(18.2)		(3.40)					(17.5)	(8.9)	

TABLE 15. Results of the Inclusion of Epistatic, Environmental, and Maternal Effects in the Full Additive Model (Chi Square, Degrees of Freedom, and p Values)

Epistasis	Environment	Maternal	χ^2	d.f.	p Value
√			299.0	235	.0030
	√		303.3	235	.0018
		√	343.5	235	.0001
√	√		273.4	225	.0152
	√	√	284.3	225	.0045
√		√	282.6	225	.0055
√	√	√	247.4	215	.0639
Full additive model			360	245	.0001

by only 16.5 and the addition of this factor did not significantly improve the model's fit at the .05 level. In the presence of a factor for epistatic effects, the addition of environmental effects improved the chi square by 26 for 10 degrees of freedom, yielding a significant improvement in fit. In the presence of environmental effects the addition of a factor for epistasis improved the chi square value by 30 for 10 degrees of freedom, also indicating a significant improvement in fit. It therefore seemed appropriate to expand the model by including factor for the effects of the epistatic interaction of genes and the effects of the environment within the uterus, which are unique to an individual pregnancy.

When maternal effects were added in the presence of these two factors, the change in the chi square value was 26 for a difference in 10 degrees of freedom. The improvement was large enough to warrant the inclusion of maternal effects in the model. With the addition of this factor, a model termed the "full genetic and environmental model" was built that could not be rejected at the .05 level of significance. This model accounted for 99% of the variance unaccounted for by the random environmental model, 95% of the variance unacccounted for by the Holt model and 71.1% of the variance unaccounted for by the full additive model. It was possible therefore, by the procedure of confirmatory factor analysis, to build a biologically plausible model which explains the inheritance pattern of individual finger ridge counts and fits significantly better than all other models of inheritance proposed in this analysis.

Table 16 gives the parameter estimates and individual environmental variances for the full genetic and environmental model. The heritabilities for the individual fingers range from .59 to .76 with an average heritability per finger of 67.5, a figure which is lower than that reported by Holt. The explanation for this discrepancy lies in the unmasking of the individual effects of the environment through multivariate analysis.

Evidence for asymmetrical expression of ridge count on both sides of the body is reflected in the fact that all left hand loadings are positive while all right hand loadings are negative. In addition, whereas the t values for loadings on the epistatic factor are in almost all cases nonsignificant, the loadings on the maternal effects factor are for the most part significant. This strongly implicates the effect of the uterine environment as an important influence on the development of ridge counts. This environment is one which is constant across pregnancies and similar in female monozygotic twins.

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TABLE 16. Factor Loadings and Random Environmental Variances for the Full Genetic and Environmental Model (With Associated t Values)

	Factor												
Finger	V_{AG}	V_{AT}	V_{A1}	V_{A2}	V_{A3}	V_{A4}	V_{AL}	V_{AR}	V_{AA}	V_M	V_E	θ_ϵ	h^2
LT	.511	.589					.337		.149	.273	.130	.194	
	(11.4)	(17.2)					(4.7)		(1.1)	(2.9)	(2.2)	(4.7)	.72
L1	.752		.115				.085		.387	.214	.028	.247	
	(10.1)		(.4)				(1.3)		(2.3)	(2.3)	(.4)	(7.9)	.71
L2	.732			.342			.083		.058	.201	−.054	.298	
	(16.5)			(7.1)			(1.4)		(.3)	(2.2)	(−.9)	(11.5)	.66
L3	.828				0.0		.120		−.216	.192	.032	.199	
	(13.3)				(0.0)		(2.2)		(−1.2)	(2.1)	(.5)	(9.1)	.76
L4	.640					.372	.214		−.161	.361	.168	.228	
	(10.9)					(5.2)	(2.8)		(−1.0)	(4.0)	(2.3)	(6.4)	.62
RT	.511	.589						−.041	.030	.452	.101	.212	
	(11.4)	(17.2)						(−.4)	(.2)	(5.5)	(1.8)	(8.3)	.59
R1	.752		.115					.012	.304	.186	−.080	.301	
	(10.1)		(.4)					(−.2)	(1.8)	(2.1)	(−1.2)	(10.0)	.66
R2	.732			.342				−.200	.113	.244	−.143	.227	
	(16.5)			(7.1)				(−2.5)	(.7)	(2.7)	(−1.8)	(6.0)	.70
R3	.828				0.0			−.097	−.256	.199	.084	.247	
	(13.3)				(0.0)			(−1.3)	(−1.4)	(2.1)	(1.2)	(9.5)	.72
R4	.640					.372		−.299	−.014	.336	.599	−.071	
	(10.9)					(5.2)		(−3.8)	(−0.1)	(3.6)	(3.7)	(−.4)	.61

Several unsuccessful attempts were made to modify the full genetic and environmental model. As a first step toward refinement, the possibility of nonorthogonality of the individual finger factors was introduced. This implied that sets of additive genes affected the count on pairs of neighboring fingers simultaneously, but did not affect the counts on the entire set of fingers with the same strength. Three covariances were estimated: those between the second and third fingers, the third and fourth fingers, and the fourth and fifth fingers. Whereas the estimates of these covariances were very large (−10.5, −24.6, and 18.9, respectively), their standard errors were also very large, and for each the associated t value was .003. The maximum likelihood estimates of these parameters did not converge, even though 250 iterations were performed. The associated chi square for the estimates obtained at the end of the 250 iterations was quite good, however, 238 for 212 degrees of freedom, yielding a p value of .103. The model was rejected, however, because the parameter estimates failed to converge.

As a second attempt at modification, the loadings were then constrained such that those for the epistasis factor were equal for homologous fingers, which paralleled the pattern of equality on six of the additive factors. The chi square value under this model was 267.4, which was an increase of 20 for 5 degrees of freedom. The associated p value for the model was .0087. These results suggested that constraining the loadings of the epistatic factor was inappropriate.

After investigating these alternative models it can be concluded that the full genetic and environmental model is a good, biologically plausible model for the explanation of inheritance patterns of individual finger ridge counts.

In order to compare the results of the Bock and Vandenberg analysis with those which may be generated by LISREL for exploratory studies, a matrix of additive genetic effects, using all of the half sib data, with the LISREL program containing 20 factors, 10 for additive genetic effects and 10 for environmental effects, was generated. The loadings on the 10 additive factors were in a triangular pattern with all fingers loading onto the first factor, L1–L4 and RT–R4 on the second, L2–L4 and RT–R4 on the third, and so on until only R4 loaded onto the tenth. A triangle of the same construction contained loadings for the environmental effects. The product of each triangular matrix with its transpose yielded one matrix of additive genetic effects and one of random environmental effects, respectively.

Table 17 gives the triangular matrix of additive loadings and Table 18 the resulting correlation matrix of genetic effects. Table 19 gives the results of a principal axis factor

TABLE 17. Matrix of Additive Genetic Factor Loadings From the LISREL Analysis

	Factor loadings									
	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	.857									
L1	.526	.708								
L2	.551	.404	.381							
L3	.536	.585	.242	.321						
L4	.518	.365	.119	.369	.443					
RT	.803	.054	−.049	−.100	.284	.275				
R1	.490	.617	−.032	−.045	−.015	.033	.085			
R2	.504	.455	.349	−.076	.062	.059	.111	.171		
R3	.431	.429	.182	.267	.039	.127	.078	−.006	0.0	
R4	.352	.432	.079	.216	.476	.069	.243	.167	0.0	0.0

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TABLE 18. Correlation Matrix of Additive Genetic Effects From the LISREL Analysis

	Factor loadings									
	LT	L1	L2	L3	L4	RT	R1	R2	R3	R4
LT	1.0									
L1	.60	1.0								
L2	.70	.83	1.0							
L3	.60	.89	.90	1.0						
L4	.60	.70	.71	.83	1.0					
RT	.89	.58	.63	.52	.66	1.0				
R1	.62	.99	.82	.85	.66	.61	1.0			
R2	.63	.83	.95	.84	.68	.63	.84	1.0		
R3	.61	.85	.87	.97	.85	.60	.83	.84	1.0	
R4	.43	.67	.62	.72	.90	.58	.67	.72	.78	1.0

TABLE 19. Results of Principal Axis Factor Analysis of the Estimated Matrix of Genetic Effects From the LISREL Analysis

	Factor[a]		
Finger	1	2	3
LT	.752	.617	−.103
L1	.916	−.171	−.229
L2	.924	−.018	−.239
L3	.938	−.235	−.056
L4	.865	−.039	.456
RT	.751	.612	.132
R1	.908	−.122	−.244
R2	.915	−.072	.173
R3	.945	−.181	.042
R4	.811	−.182	.499

[a]Portion of variance explained by each factor: 1, 76.6%; 2, 9.3%; 3, 6.9%.

analysis where three factors account for 92.8% of the variance. As with the results of the Bock and Vandenberg analysis, the first factor, which accounts for 76.6% of the variance, is a general additive factor contributing substantially to the ridge counts on each of the ten fingers, with the three middle fingers of each hand loading onto it most heavily. The second factor influences the thumbs primarily, and the third influences the little fingers. Results from the Bock and Vandenberg analysis indicate one factor accounting for the thumb and little finger, although the signs of their weights on that factor are opposite. Weights of homologous fingers are nearly equal for all three factors. The results agree substantially with those of Nance et al [36].

5. SUMMARY AND CONCLUSIONS

Two methods have been studied for extending the half-sib model, which was developed by Nance and Corey [34] for the genetic analysis of univariate traits, to include the analysis of multivariate traits. The methods are adaptations of the Bock and Vandenberg procedure [4] and the form of confirmatory maximum likelihood factor analysis which

was developed by Jöreskog and Sörbom for the LISREL IV program [22]. These methods were applied to sex-adjusted individual finger ridge count data from the offspring of monozygotic twins.

The Bock and Vandenberg procedure was applied to the eigenvalues and eigenvectors from a nested analysis of variance on 30 balanced male twin kinships. The result was a matrix of pure genetic effects which was at least positive semidefinite, and therefore appropriate for factor analytic procedures. Principal components analysis revealed two substantial genetic factors, one with a strong impact on the ridge counts of all ten fingers, with the largest loadings on the three central fingers of each hand, and the other influencing the thumbs and fifth fingers wtih opposite signs. In both cases, the factor loadings of homologous fingers were nearly equal.

Employing the Bock and Vandenberg procedure to analyze multivariate data from MZ twin kinship has both positive and negative features. Its greatest strength is that it is easy to program with the Nested, Matrix, and Factor Procedures of the Statistical Analysis System package [see 44]. Multivariate half-sib data on any traits can be quickly explored for genotypic associations with the availability of this package or others like it. The exploratory findings from this analysis, the LISREL analysis, and the Bock and Vandenberg analysis on MZ and DZ twin pairs, as reported by Nance et al [36] are in agreement. This attests to the validity of the results from the two procedures. Such strong agreement may not be the case for other genetic structures, however, and analysis of other sets of traits or analyses on simulated data should clarify the cases under which the procedures produce concordant results.

A negative feature of the Bock and Vandenberg procedure is that it wastes much of the data taken from individuals who attend the Twin Clinic. Both male and female kinships are routinely ascertained, with equal frequencies, although in this analysis we have examined the results from male kinships only. In addition, a substantial number of the male kinships either do not meet the criterion of at least two individuals in each sibship, or else have larger sibships containing individuals who must be excluded from the analysis. One might consider conducting an analysis on the eigenvalues and eigenvectors of the among component from balanced female kinships, but this would require the assumption of no maternal effects for the traits under study. Analysis of the eigenvalues and eigenvectors of the component between sibships nested within female kinships would not be biased by maternal effects, but would be substantially influenced by the presence of gene interactions both within and between loci. Therefore, without very stringent assumptions, only a small portion of the available data is appropriate for this analysis.

All the data from the offspring of 97 monozygotic twin pairs was analyzed in two ways using the LISREL IV program. In one mode, the program served to generate a matrix of pure genetic effects which was positive semidefinite and appropriate for exploratory factor analytic procedures. Results from this analysis and those obtained by the Bock and Vandenberg procedure are concordant. If results are also concordant under other genetic structures, one may conclude that the LISREL analysis can be used in lieu of the previous analysis to generate the same results. LISREL is not wasteful of data as is the Bock and Vandenberg analysis. In addition, the same LISREL procedure can be used to generate matrices of pure environmental, maternal and interactive genetic effects, which are also suitable for exploratory factor analyses. One must be concerned, however, whether all of the parameters in the model generating the matrices are identified and whether their estimates will converge. Trial and error is, at present, the most appropriate way to explore these problems.

In its second mode, the LISREL IV program served to test hypotheses about proposed genetic and environmental models for inheritance patterns of individual finger ridge counts. After some investigation, a model containing eight additive genetic factors, eleven environmental factors, one epistatic factor and one maternal factor was constructed which could not be rejected at the .05 level of significance. Although the model was only marginally acceptable with a p value of .06, the Tucker and Lewis [49] reliability coefficient indicated that this model accounted for 99% of the variance in ridge counts which could not be accounted for by the model containing only random environmental effects. The difficulty encountered in constructing a model which could not be rejected by the chi square statistic reflects a problem with the use of confirmatory factor analysis for multivariate model fitting. Any deviation from the "true" model by the proposed model will increase the value of this statistic, so that finding a model which fits well according to this criterion becomes a significant challenge. This does indicate, however, that once a model fits, one can feel secure that it provides a good explanation of the traits under analysis.

In constructing a multivariate genetic model the proposed factors should be developed along two separate lines. The effects that influence the trait must be chosen, and the structures of these effects hypothesized as well. In the analysis on ridge counts, prior research indicated that additive genetic and individual environmental effects are primarily responsible for the expression of the trait on each of the fingers. Therefore, the structures of these two effects were proposed first, and the addition of the general environmental, maternal, and epistatic factors followed. Conceivably, another plan for building the model would have led to different results. This is a hazard of the model fitting procedure which cannot be avoided, and the researcher is advised to use insight into the biological processes involved to discriminate between alternative models which do fit.

The genetic and environmental model which best fits the data on ridge counts indicates, as have other genetic analyses, that a substantial portion of the determination of the ridge counts on the ten fingers may be attributed to a common set of additive genes which influence the three middle fingers of both hands most strongly. The thumbs and little fingers are subject to the impact of other additive genes, as well as maternal and random environmental effects, and there may be maternal effects influencing the ridge counts on the six central fingers as well. One may therefore conceive of the hand as having three inner fingers and two outer fingers. Ridge counts on the inner fingers are primarily influenced by a common set of additive genes, whereas counts on the outer fingers are additionally controlled by different sets of additive genes and are vulnerable to the environmental impacts within the uterus.

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APPENDIX A

```
**********
LISREL IV PROGRAM FOR THE FULL ADDITIVE MODEL WITH MATERNAL EFFECTS
**********
JOB CARD
//EXEC LISREL, SIZE = ---, MIN = ---
ANALYSIS OF BETWEEN MEAN SQUARES (FEMALES)
DA NI = 10 NO = 59 MA = CM NG = 5
LA
*
'LT' 'L1' 'L2' 'L3' 'L4' 'RT' 'R1' 'R2' 'R3' 'R4'
CM SY
*
**********
DATA CARDS GO HERE WITH THE MATRIX IN LOWER TRIANGULAR FORM
**********
MO NY = 10 NE = 9 TE = DI, FR PS = SY, FI LY = FU,FI
```

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```
FR LY(1,1) LY(2,1l) LY(3,1) LY(4,1) LY(5,1) LY(6,10) LY(7,10) LY(8,10)
FR LY(9,10) LY(10,10)
LY(1,2) LY(2,2) LY(3,2) LY(4.2) LY(5,2)
FR LY(6,3) LY(7,3) LY(8,3) LY(9,3) LY(10,3)
FR LY(1,4) LY(6,4)
FR LY(2,5) LY(7,5)
FR LY(3,6) LY(8,6)
FR LY(4,7) LY(9,7)
FR LY(5,8) LY(10,8)
EQ LY(1,1) LY(6,1)
EQ LY(2,1) LY(7,1)
EQ LY(3,1) LY(8,1)
EQ LY(4,1) LY(9,1)
EQ LY(5,1) LY(10,1)
EQ LY(1,4) LY(6,4)
EQ LY(2,5) LY(7,5)
EQ LY(3,6) LY(8,6)
EQ LY(4,7) LY(9,7)
EQ LY(5,8) LY(10,8)
ST 1.0 PS(1,1) PS (2,2) PS(3,3) PS(4,4) PS(5,5) PS(6,6) PS(7,7) PS(8,8) PS(9,9)
*****************************************************
THE NEXT CARD GIVES THE VALUE OF BETA FOR THE BETWEEN
SIBSHIPS WITHIN FEMALE KINSHIPS MEAN SUMS OF SQUARES AND
CROSS PRODUCTS MATRIX ANALYSIS. THE VALUE OF BETA IS
CALCULATED IN THE FOLLOWING WAY FOR THIS GROUP FOR THE
ADDITIVE GENETIC EFFECTS:

     1/2 VA + (b4)(1/4 VA) = x (FROM TABLE 2)

     BETA FOR VA IS 1/SQUARE ROOT OF X

  HERE: [1/2 + b4(1/4)]VA = [.5 + 2.279(.25)]VA = [.5 + .5698]VA =
1.0698VA

     BETA = 1/SQUARE ROOT OF 1.0698 = .9669
*****************************************************
ST .9669 BE (1,1) BE(2,2) BE(3,3) BE(4,4) BE(5,5) BE(6,6) BE(7,7) BE(8,8)

*****************************************************
THE NEXT CARD GIVES THE VALUE OF BETA FOR MATERNAL EFFECTS.
SINCE THERE ARE NO MATERNAL EFFECTS FOR THIS GROUP WE
ENSURE THAT THE BETA MATRIX IS NON-SINGULAR BY SETTING THE
VALUE OF BETA TO 1.0
*****************************************************
ST 1.0 BE(9,9)
ST .5 ALL
OU PM TV MR
ANALYSIS OF WITHIN SIBSHIPS MEAN SQUARES (TOTAL SAMPLE)
```

```
DA NO = 307
LA
*
'LT' 'L1' 'L2' 'L3' 'L4' 'RT' 'R1' 'R2' 'R3' 'R4'
CM SY
*
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ENTER LOWER TRIANGULAR MATRIX OF MEAN SUMS OF SQUARES AND
CROSSPRODUCTS HERE.
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
MO BE = SP TE = IN PS = IN LY = IN
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
TO OBTAIN THE VALUE OF BETA FOR THE ADDITIVE EFFECTS FOR THIS
GROUP USE THE SAME PROCEDURE THAT WAS USED IN THE PREVIOUS
GROUP FROM TABLE 2 THE MATRIX OF SUMS OF SQUARES AND
CROSS-PRODUCTS IS EQUAL TO:

        1/2 VA + VEW.

SO, BETA FOR VA IS 1/SQUARE ROOT OF 1/2 = SQUARE ROOT OF 2 =
1.414.
AS BEFORE, THE VALUE OF BETA FOR THE MATERNAL EFFECTS IS
TAKEN AS 1.
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ST 1.414 BE(1,1) BE(2,2) BE(3,3) BE(4,4) BE(5,5) BE(6,6) BE(7,7) BE(8,8)
ST 1.0 BE(9,9)
ST .5 ALL
OU PM TV MR
ANALYSIS OF AMONG MEAN SQUARES (FEMALES)
DA NO = 58
LA
*
'LT' 'L1' 'L2' 'L3' 'L4' 'RT' 'R1' 'R2' 'R3' 'R4'
CM SY
*
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ENTER MEAN SUMS OF SQUARES AND CROSS PRODUCTS MATRIX FOR
AMONG FEMALE KINSHIPS IN LOWER TRIANGULAR FORM HERE.
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
MO BE = SP TE = IN PS = IN LY = IN
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
THE NEXT CARD FREES UP THE PARAMETERS FOR THE MATERNAL
EFFECTS WHICH WILL BE ESTIMATED FOR THE FIRST TIME IN THIS
ANALYSIS FOR THIS GROUP.
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
FR LY(1,9) LY(2,9) LY(3,9) LY(4,9) LY(5,9) LY(6,9) LY(7,9) LY(8,9) LY(9,9)
FR LY(10,9)
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
```

THE VALUES FOR THE BETA MATRIX ARE CALCULATED HERE AS BEFORE.
FOR THE ADDITIVE EFFECTS:

1/2 VA + b5(1/4 VA) + b6(1/4 VA) = [.5 + 2.626(.25) + 4.898(.25)] VA = 2.381 VA.
SO, BETA = 1/SQUARE ROOT OF 2.381 = .6481

```
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ST .6481 BE(1,1) BE(2,2) BE(3,3) BE(4,4) BE(5,5) BE(6,6) BE(7,7) BE(8,8)
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
```

TO CALCULATE THE VALUE OF BETA FOR MATERNAL EFFECTS FOR THIS GROUP, REFER TO TABLE 2 WE HAVE THE EXPECTED VALUE OF THE 4E MEAN SUMS OF SQUARES AND CROSS PRODUCTS MATRIX AS:

b6 VM = 4.898

SO, BETA FOR MATERNAL EFFECTS FOR THIS GROUP IS 1/SQUARE ROOT 4.898 = .4519

```
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ST .4519 BE(9,9)
ST .5 ALL
OU PM TV MR
ANALYSIS OF BETWEEN SIBSHIPS MEAN SQUARES (MALES)
DA NO = 48
LA
*
'LT' 'L1' 'L2' 'L3' 'L4' 'RT' 'R1' 'R2' 'R3' 'R4'
CM SY
*
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ENTER LOWER TRIANGULAR MATRIX OF MEAN SUMS OF SQUARES AND CROSSPRODUCTS FOR THIS GROUP HERE.
* * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
MO = SP TE = IN PS = IN LY = IN
EQ LY(3,1,9) LY(1,9)
EQ LY(3,2,9) LY(2,9)
EQ LY(3,3,9) LY(3,9)
EQ LY(3,4,9) LY(4,9)
EQ LY(3,5,9) LY(5,9)
EQ LY(3,6,9) LY(6,9)
EQ LY(3,7,9) LY(7,9)
EQ LY(3,8,9) LY(8,9)
EQ LY(3,9,9) LY(3,9)
EQ LY(3,10,9) LY(10,9)
ST .9720 BE(1,1) BE(2,2) BE(3,3) BE(4,4) BE(5,5) BE(6,6) BE(7,7) BE(8.8)
ST .6691 BE(9,9)
ST .5 ALL
OU PM TV MR
```

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```
ANALYSIS OF AMONG KINSHIPS MEAN SQUARES (MALES)
DA NO = 47
LA
*
'LT' 'L1' 'L2' 'L3' 'L4' 'RT' 'R1' 'R2' 'R3' 'R4'
CM SY
*
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
ENTER DATA HERE.
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
MO BE = SP TE = IN PS = IN LY = PS
ST .6538 BE(1,1) BE(2,2) BE(3,3) BE(4,4) BE(5,5) BE(6,6) BE(7,7) BE(8,8)
ST .6421 BE(9,9)
ST .5 ALL
OU PM TV MR
//
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
 * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * * *
```

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