AN ABSTRACT OF THE THESIS OF

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Title: <u>Statistical Properties of Estimators of Genetic</u> <u>Correlation</u> Abstract approved: Redacted for Privacy *I* V Steven J. Knapp

The genetic correlation coefficient (ρ_g) is an important and widely used parameter in quantitative genetics and plant and animal breeding. Multivariate analysis of variance (MANOVA), restricted maximum likelihood (REML), and maximum likelihood (ML) methods can be used to estimate the variances and covariances used to estimate ρ_g . The statistical properties of point and interval estimators of ρ_g have not yet been investigated.

Our objectives were to investigate the statistical properties of MANOVA, REML, and ML estimators of ρ_g and evaluate normal-approximation parametric, jackknife, and bootstrap and percentile and bias-corrected percentile bootstrap intervals of MANOVA and ML estimators of ρ_g . This investigation was done using computer simulation. Simulations were done using a balanced one-way linear model with two correlated traits bivariate normally distributed.

MANOVA estimates of ρ_g were approximately normally distributed. ML and REML estimates of ρ_g were also

approximately normally distributed when $\rho_g = 0.1$, but were skewed when $\rho_g = 0.5$ or 0.9. Biases of ML and REML estimators were greater than those of the MANOVA estimator when heritability and sample size were small, but they were similar when sample size was large. The variance estimators of Scheinberg (1966) and Falconer (1981) were not valid. Empirical estimates of the variance of MANOVA estimator of ρ_g were consistently greater than those of ML and REML estimators. Jackknifing and bootstrapping did not decrease bias for both MANOVA and ML estimators. A valid estimate of the variance of $\hat{\rho}_g$ may be obtained using bootstrapping. Using of ML or REML estimator along with bootstrapping is recommended for estimating genetic correlation.

Estimated coverage probabilities (ECP) for parametric intervals and normal-approximation nonparametric intervals were significantly different from stated coverage probabilities (SCP). Parametric intervals often were wide and had negative lower bounds. ECPs for the percentile bootstrap interval were relatively close to SCPs. ECPs of the bias-corrected bootstrap interval were close to SCPs. Intervals of MANOVA estimators were consistently wider than those of ML estimators. The biascorrected bootstrap percentile interval of the ML estimator should be used for estimating confidence intervals for genetic correlation. The number of genotypes used was more important for reducing interval lengths than the number of replications used.

Statistical Properties of Estimators of Genetic Correlation

by

Ben-Hui Liu

A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Completed May 2, 1990 Commencement June 1990 APPROVED:

Redacted for Privacy

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Date thesis is presented <u>May 2, 1990</u>

In dedication to my wife, my son, my parents, and grand parents.

I wish to express my sincere gratitude to my major Professor Dr. Steven J. Knapp, for his guidance, encouragement, support and friendship throughout the course of my graduate study and preparation of this thesis.

I thank the members of my graduate committee, Drs. Thomas W. Adams, David Birkes, Peter J. Bottomley, and Patrick M. Hayes for their time and guidance.

I am also grateful to all colleagues on the Cophea Project for their friendship and secretaries in Crop Science Department for their help and friendship.

Special thanks to my wife, Qiang, for her love, understanding, and encouragement.

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Statistical Properties of Estimators of Genetic Correlation

CHAPTER 1. INTRODUCTION

Genetic correlation (ρ_g) is an important and widely used parameter in population and quantitative genetics and plant and animal breeding. Estimates of ρ_g are needed, for example, to estimate indirect and correlated selection responses (Falconer 1981) and selection indexes (Baker 1986) and to determine how fitness is affected by selection against different traits (Lande 1984).

The variances and covariances used to estimate ρ_g can be estimated using multivariate analysis of variance (MANOVA), restricted maximum likelihood (REML) (Amemiya 1985), and maximum likelihood (ML) (Klotz and Putter 1969) methods. It is well known that MANOVA has the serious limitation of yielding non-positive definite (NPD) estimates of genetic variance-covariance matrices (Σ_g) (Hill and Thompson 1978). The probability of NPD estimates is a function of the probability of negative estimates of the variances and the probability of estimates outside the parameter space (-1.0 < $\hat{\rho}_g < 1.0$); thus, MANOVA has the unsatisfactory properties of yielding meaningless estimates of ρ_g ($\hat{\rho}_g > 1.0$ or $\hat{\rho}_g < -1.0$) or of ρ_g being inestimable because of negative variances. REML and ML estimation of covariance components is straightforward using a one-way linear model (Amemiya 1985; Klotz and Putter 1969); however, REML and ML algorithms have not been developed to analyze multivariate linear models of greater complexity (Rao and Kleffe 1988). Because of this, MANOVA has been widely and nearly exclusively used to estimate ρ_8 . Is this by default or are the properties of MANOVA estimators of ρ_8 superior to those of REML or ML estimators of ρ_8 ? This question has been investigated for variances (Swallow and Monahan 1984), but not for covariances or their functions.

Several questions about the properties of estimators of ρ_8 have not been examined. How are MANOVA, REML, and ML estimates of ρ_8 distributed? What is the joint probability of negative MANOVA estimates of variances used to estimate ρ_8 and the probability of MANOVA ρ_8 estimates outside the parameter space, and how are they affected by heritability, ρ_8 , and sample size? Are MANOVA, REML, and ML estimators of ρ_8 biased? Are jackknifing and bootstrapping effective methods to estimate and correct for the bias of estimates of ρ_8 ? Are parametric, jackknife, and bootstrap estimators of the variance of ρ_8 valid?

Parametric interval estimators have been difficult to define for many genetic parameters because their distributions are unknown. This has been shown for expected selection response (Knapp et al. 1989; Bridges et al. 1990), and is a problem for genetic correlation (ρ_8) as well.

Approximate parametric estimators of the variance of genetic correlation have been described (Falconer 1981; Reeve 1955; Robertson 1959; Scheinberg 1966; Tallis 1959) but these estimators have not been widely used, perhaps because they are complex and their validity is uncertain. It is not known, for example, how well these estimators approximate the true sampling variation of estimates of genetic correlation. Furthermore, they strictly apply to MANOVA estimates of genetic correlation. Other methods are needed for genetic correlation estimated using ML or REML estimates of variances and covariances.

Fast, efficient, and inexpensive computing technology has made it practical and feasible to apply data resampling methods, especially bootstrapping, to a wide range of statistical inference problems arising in population and quantitative genetics. Bootstrapping has been used, for example, to estimate cumulative density functions (CDFs) and bias-corrected percentile (BCP) intervals of mating systems parameters (Knapp et al. 1991) and genetic correlation coefficients (Riska et al. 1990). Delete-one jackknifing has been used to estimate intervals for heritability, expected selection response, and other genetic parameters (Knapp et al. 1989; Mitchell-Olds and Bergelson 1990).

Jackknifing and bootstrapping are tremendously versatile statistical tools because they can be applied to estimation problems where the distribution of the parameters are unknown

or the validity of parametric methods are inadequate or sensitive to distributional or model assumptions (Miller 1974; Efron 1982), e.g., the estimation of intervals for variances (Miller 1974) and family-mean heritability (Arvesen and Schmitz 1970; Knapp et al. 1989). Their strength is magnified by their simplicity -- the bootstrap method is applied the same regardless of the parameter being estimated. It is this versatility and power which led us to investigate the validity of these methods for estimating intervals for genetic correlation coefficients. Furthermore, there are no known parametric methods for estimating variances and intervals of ML and REML estimators of genetic correlation.

This thesis includes two papers. In the first paper, we report a Monte Carlo simulation study done to investigate the statistical properties (these are distribution, bias, and variance) of MANOVA, ML, and REML point estimators of ρ_g . In the second paper, we report a simulation study done to investigate the validity of interval estimators of ρ_g ; these estimators are normal-approximation parametric, jackknife, and bootstrap and percentile and bias-corrected percentile bootstrap intervals.

CHAPTER 2

STATISTICAL PROPERTIES OF MANOVA, REML, AND ML ESTIMATORS OF GENETIC CORRELATION

Abstract

A suite of traits may determine the fitness or biological value of an individual or family. An understanding of the interrelationships among traits is gained by estimating their genetic correlations (ρ_g) . Multivariate analysis of variance (MANOVA), restricted maximum likelihood (REML), and maximum likelihood (ML) methods can be used to estimate the variances and covariances used to calculate $\hat{\rho}_{g}$. The properties of the estimators are well known but the properties of different estimators of $\rho_{\rm g}$ have not yet been investigated. In this paper we describe a Monte Carlo simulation study of the statistical properties of MANOVA, REML, and ML estimators of ρ_g . The probability of negative MANOVA estimates of genetic variances was significantly decreased by increasing heritability and sample size, but was not significantly affected by the magnitude of true ρ_{g} and environment correlation (ρ_{g}). The main effect of number of replications (n) was significantly greater than the main effect of number of genotypes (r). The probability of MANOVA estimates greater than 1.0 or less -1.0 ranged from 0.0 to 0.089, depending on the magnitude of ρ_{g} , ρ_{e} , heritability, and sample size. MANOVA estimates were approximately normally distributed regardless of the value of $\rho_{\rm g},\ \rho_{\rm e},$ heritability, and sample size. ML and REML estimates were also approximately normally distributed when $\rho_g = 0.1$, but were skewed when $\rho_g = 0.5$ or 0.9. Biases of ML and REML

estimators were greater than MANOVA estimators when heritability, n, and r were low, but were similar when sample size was large. The variance estimators of Scheinberg (1966) and Falconer (1981) were not valid. Estimated variances of MANOVA estimators were consistently greater than those of ML and REML estimators. Bias was not reduced by jackknifing and bootstrapping. Valid estimates of the variance of ρ_g may be obtained by using bootstrapping. ML or REML estimator of ρ_g should be used.

Key Words: bootstrap, jackknife, maximum likelihood, restricted maximum likelihood, genetic correlation.

Introduction

The fitness or biological or economic worth of an individual or family is often determined by several traits. An understanding of the interrelationships among these traits is gained by estimating their genetic correlations (ρ_g) . These estimates are needed to make inferences about the way traits are affected by selection and other biological forces. Estimates of ρ_g are needed, for example, to estimate indirect and correlated selection responses (Falconer 1981), selection indexes (Baker 1986), and to determine how fitness is affected by selection against different traits (Lande 1984).

The variances and covariances used to estimate ρ_8 can be estimated using multivariate analysis of variance (MANOVA), restricted maximum likelihood (REML) (Amemiya 1985), and maximum likelihood (ML) (Klotz and Putter 1969) methods. REML and ML estimation of covariance components is straightforward when a one-way linear model is appropriate (Amemiya 1985; Klotz and Putter 1969); however, REML and ML algorithms have not been developed to analyze multivariate linear models of greater complexity (Rao and Kleffe 1988). Because of this, MANOVA has been widely and nearly exclusively used to estimate ρ_8 . Is this by default, or are the properties of MANOVA estimators of ρ_8 superior to those of REML or ML estimators of ρ_8 ? This question has been investigated for variances (Swallow and Monahan 1984), but not for covariances or their functions. If analysis of variance (ANOVA) is used to estimate genetic variances, then the estimates may be negative. This problem is well known and unavoidable (Searle 1970). REML and ML estimation methods have the statistically superior property of yielding solutions within the parameter space $(0.0 < \sigma^2 < \text{infinity})$ (Rao and Kleffe 1988). Using REML or ML methods, estimates of variances are calculated by solving systems of nonlinear equations. Different algorithms have been proposed and developed to do this, but their solutions are not necessarily consistent (Harville 1977, Rao and Kleffe 1988) and they do not guarantee solutions which are ML estimates (Harville 1977).

ML estimators are those which maximize the full likelihood function over the parameter space (Rao and Kleffe 1988). They are biased and may not be consistent (Harville 1977; Rao and Kleffe 1988). The simulation studies of Swallow and Monahan (1984) illustrate the size and seriousness of the bias of ML estimates of variances; however, they applied a straightforward bias correction which led to nearly unbiased estimates. The correction was the multiplier (t - 1)/t where t is the number of treatment classes in a one-way linear model (Swallow and Monahan 1984). As t becomes large, the effect of the multiplier is diminished.

The variances of ML estimators of variance are usually significantly less than those of ANOVA and REML estimators,

but the variance reduction is caused by bias (Swallow and Monahan 1984). Correcting for bias increases the variance and eliminates the superiority of ML estimators (Swallow and Monahan 1984). Because of this, Swallow and Monahan (1984) urged the use of ML estimators when $\sigma_g^2/\sigma_e^2 < 0.5$ and ANOVA estimators when $\sigma_g^2/\sigma_e^2 > 0.5$, where σ_g^2 and σ_e^2 are the between and within class variances in a one-way model. The main shortcoming of the ANOVA method, i.e., negative estimates, is greatly diminished when $\sigma_g^2/\sigma_e^2 > 0.5$.

MANOVA has the serious limitation of yielding non-positive definite (NPD) estimates of genetic variance-covariance matrices (Σ_s) (Hill and Thompson 1978). The probability of NPD estimates is a function of the probability of negative estimates of the variances and the probability of estimates outside the parameter space (-1.0 < $\hat{\rho}_{g}$ < 1.0); thus, MANOVA has the unsatisfactory properties of yielding meaningless estimates of $\rho_{\rm g}$ ($\hat{\rho}_{\rm g}$ > 1.0 or $\hat{\rho}_{\rm g}$ < -1.0) or of ρ_{g} being inestimable because of negative variances. Hill and Thompson (1978) estimated the probability of NPD estimates of Σ_g for $\rho_g = 0.0$ using analytical methods and simulation. This probability ranged from 0.0 to 100.0% (Hill and Thompson 1978), increasing as the number of dependent variables increased and heritability decreased. In this paper, we report estimates of the probabilities which comprise the probability of NPD estimates of Σ_s --the probability of negative estimates of either of the variances

used to estimate ρ_g and the probability of estimates of ρ_g outside the parameter space--and estimate the effect of ρ_g and ρ_s on the probabilities, which has not been done.

Several questions about the properties of estimators of $\rho_{\rm g}$ have not been examined. How are MANOVA, REML, and ML estimators of $\rho_{\rm g}$ distributed? What is the joint probability of negative MANOVA estimates of variances used to estimate $\rho_{\rm g}$ and the probability of MANOVA $\rho_{\rm g}$ estimates outside the parameter space, and how are they affected by heritability, $\rho_{\rm g}$, and sample size? Are MANOVA, REML, and ML estimators of $\rho_{\rm g}$ biased? Are jackknifing and bootstrapping effective methods to estimate and correct for the bias of estimates of $\rho_{\rm g}$? Are parametric, jackknife, and bootstrap estimators of the variance of $\rho_{\rm g}$ valid? In this paper, we report on a Monte Carlo simulation study done to investigate these questions.

Materials and Methods

Model: A suitable linear model for a completely randomized experimental design with two correlated traits A and B is

$$X_{aij} = \mu_a + G_{ai} + \epsilon_{aij}$$

$$X_{bij} = \mu_b + G_{bi} + \epsilon_{bij}$$
(1)

where X_{aij} and X_{bij} are observations on the jth replication of the ith genotype for traits A and B respectively, i = 1, 2, ..., n, j = 1, 2, ..., r, n is the number of genotypes, r is the number of replications, μ_a and μ_b are population means, G_{ai} and G_{bi} are random effects of the ith genotype; and ϵ_{aij} and ϵ_{bij} are residual associated with the jth sample of the ith genotype. G_{ai} and G_{bi} are correlated random variables with zero means and a variance-covariance matrix

$$\Sigma_{g} = \begin{bmatrix} \sigma_{ga}^{2} & \sigma_{gab} \\ & \sigma_{gb}^{2} \end{bmatrix}$$

where $\rho_g = \sigma_{gab} / (\sigma_{ga}\sigma_{gb})$ is the genetic correlation coefficient between traits A and B. ϵ_{aij} and ϵ_{bij} are correlated random variables with zero means and variancecovariance matrix

$$\Sigma_{e} = \begin{bmatrix} \sigma_{ea}^{2} & \sigma_{eab} \\ & & \\ & \sigma_{eb}^{2} \end{bmatrix}$$

where $\rho_{e} = \sigma_{eab} / (\sigma_{ea}\sigma_{eb})$ is the environmental correlation coefficient. $H_{a} = \sigma_{ga}^{2} / (\sigma_{ga}^{2} + r^{-1}\sigma_{ea}^{2})$ and $H_{b} = \sigma_{gb}^{2} / (\sigma_{gb}^{2} + r^{-1}\sigma_{eb}^{2})$ are family-mean heritabilities of traits A and B, respectively. We used S_g and S_e to denote the matrices of mean square for genotypes and error, respectively. Here

$$\mathbf{S}_{g} = \begin{bmatrix} \mathbf{MS}_{ga} & \mathbf{MS}_{gab} \\ & \mathbf{MS}_{gb} \end{bmatrix}$$

and
$$\mathbf{S}_{e} = \begin{bmatrix} \mathbf{MS}_{ea} & \mathbf{MS}_{eab} \\ & \mathbf{MS}_{eb} \end{bmatrix}$$

where MS_{ga} , MS_{gb} , and MS_{gab} are genotype mean squares for traits A, B, and A by B, respectively; MS_{ea} , MS_{eb} , and MS_{eab} are error mean squares for trait A, B, and A by B, respectively. The expected mean squares of genotypes and error are Σ_e + $r\Sigma_g$ and Σ_e , respectively.

Estimation methods: Parameters were estimated using MANOVA, ML, and REML. In addition, they were estimated by delete-one jackknifing (Miller 1974) and bootstrapping (Efron 1982) MANOVA and ML estimators. Bootstrapping was done using 100 and 500 bootstrap samples.

MANOVA estimators of variances and covariances are

 $\hat{\sigma}_{ea}^{2} = MS_{ea}, \quad \hat{\sigma}_{eb}^{2} = MS_{eb}, \quad \hat{\sigma}_{eab} = MS_{eab},$ $\hat{\sigma}_{ga}^{2} = r^{-1}(MS_{ga} - MS_{ea}),$ $\hat{\sigma}_{gb}^{2} = r^{-1}(MS_{gb} - MS_{eb}),$ $\hat{\sigma}_{gab} = r^{-1}(MS_{gab} - MS_{eab}).$

 ho_g was estimated using $\hat{
ho}_g = \hat{\sigma}_{gab} / (\hat{\sigma}_{ga}^2 \hat{\sigma}_{gb}^2)^4$. If $\hat{\sigma}_{ga}^2 > 0$ and $\hat{\sigma}_{gb}^2 > 0$, then ρ_g is estimable. If $\hat{\sigma}_{ga}^2 < 0$ or $\hat{\sigma}_{gb}^2 < 0$, then $\hat{\rho}_g$ is undefined. Undefined estimates were treated as missing values.

ML and REML estimators of genetic variance and covariance

components are ordinarily estimated using iterative methods; however, for the balanced one-way model, Klotz and Putter (1969) and Amemiya (1985) described linear solutions for ML and REML estimation, respectively. The ML genetic variancecovariance matrix was estimated using

$$\hat{\boldsymbol{\Sigma}}_{\mathbf{g}} = (\mathbf{n}\mathbf{r})^{-1} \mathbf{S}_{\mathbf{t}} (\mathbf{S}_{\mathbf{t}}^{-} \mathbf{A})^{+}$$
(2)

where $\mathbf{S}_t = (n - 1)\mathbf{S}_g + n(r - 1)\mathbf{S}_g$, $\mathbf{A} = (n - 1)\mathbf{S}_g - n\mathbf{S}_g$, \mathbf{S}_t is a generalized inverse of \mathbf{S}_t , and $(\mathbf{S}_t \mathbf{A})^+$ is the positive semidefinite part of the matrix $\mathbf{S}_t \mathbf{A}$.

We used the method of Amemiya (1985) to develop an algorithm for REML estimation of variance-covariance for a balanced one-way model. The matrix L satisfying $\mathbf{L}'\mathbf{S}_{e}\mathbf{L} = \mathbf{I}$ was found using Cholesky decomposition of \mathbf{S}_{e} where $\mathbf{L} = \mathbf{U}^{-1}$ and $\mathbf{S}_{e} = \mathbf{U}'\mathbf{U}$. The eigenvalues of \mathbf{S}_{g} in the metric of \mathbf{S}_{e} ($|\mathbf{S}_{g} - \lambda \mathbf{S}_{e}| = 0$) are the eigenvalues of $\mathbf{L}'\mathbf{S}_{g}\mathbf{L}$. The matrix Q of orthonormal eigenvectors of $\mathbf{L}'\mathbf{S}_{g}\mathbf{L}$ was used to find $\mathbf{P} = \mathbf{L'}^{-1}\mathbf{Q}$. The non-negative definite partition of $\mathbf{S}_{g} - \mathbf{S}_{e}$ is equivalent to the part of $\mathbf{L}'\mathbf{S}_{g}\mathbf{L}$ having eigenvalues greater than 1.0. The genetic variance-covariance matrix was estimated using

$$\hat{\Sigma}_{\mathbf{g}} = \mathbf{r}^{-1} \mathbf{P}_{\mathbf{k}} (\Lambda_{\mathbf{k}} - \mathbf{I}) \mathbf{P}_{\mathbf{k}}'$$
(3)

where Λ_k is diag $\{\lambda_1, \lambda_2, \ldots, \lambda_k\}$ and P_k is a matrix of the first k columns of P, $\lambda_1, \lambda_2, \ldots, \lambda_k$ are the first k eigenvalues of L'S_kL.

We used delete-one jackknifing MANOVA and ML estimators to estimate ρ_g (Miller 1974). Parameters were estimated from n - 1 data sets of n genotypes where the ith genotype had been deleted. For each of the n data sets a different genotype was deleted.

Pseudovalues (Miller 1968) were estimated using

 $\tilde{\rho}_{g(i)} = n\hat{\rho}_{g} - (n - 1)\hat{\rho}_{g(i)}$

where $\hat{\rho}_{g}$ is the MANOVA or ML estimate from the original data and $\hat{\rho}_{g(i)}$ is the MANOVA or ML estimate from the data missing the ith genotype. ρ_{g} was estimated using the pseudovalue mean

$$\bar{\rho}_{g} = \Sigma \tilde{\rho}_{g(i)} / n$$

and the variance $\overline{\rho}_{g}$ was estimated by

 $\hat{\sigma}_{J}^{2} = \Sigma (\tilde{\rho}_{g(1)} - \bar{\rho}_{g})^{2} / [n(n-1)], \qquad (4)$

respectively.

If MANOVA estimates of $\hat{\sigma}_{ga}^2$ or $\hat{\sigma}_{gb}^2$ were less than 0.0, then jackknifing was not done ($\hat{\rho}_g$ is not defined when $\hat{\sigma}_{ga}^2 < 0$ or $\hat{\sigma}_{gb}^2 < 0$). Even when MANOVA estimates of the variance from the original data were greater than 0.0, estimates from resampled data were not necessarily greater than 0.0. Pseudovalue means and variances were estimated from the fraction of defined estimates. These problems do not plague ML estimators. Pseudovalue means and variances estimated using MANOVA and ML methods are hereafter referened to jackknife MANOVA and ML estimators, respectively.

Bootstrapping was also used to estimate ρ_g and the variance of ρ_g (Efron 1982). A bootstrap sample was drawn by randomly sampling n genotypes with replacement, where each genotype had a probability mass of 1/n. The number of

bootstrap samples (b) drawn was set at 100 and 500. $\rho_{\rm g}$ was estimated using the bootstrap mean

$$\bar{\rho}_{g} = \Sigma \hat{\rho}_{g(i)} / b$$

and the variance $\bar{\rho}_{g}$ was estimated by

$$\hat{\sigma}_{\rm B}^{\ 2} = \Sigma \left(\hat{\rho}_{\rm g(i)} - \bar{\rho}_{\rm g} \right)^2 / (b - 1), \tag{5}$$

respectively, where $\rho_{g(i)}$ is a MANOVA or ML estimate from the ith bootstrap sample.

Bootstrap means and variances were not estimated when MANOVA estimates of the variances component were negative. Repeated resampling was done to get b defined estimates from resampled data where necessary. Bootstrap means and variances estimated using MANOVA and ML are hereafter referened to as bootstrap MANOVA and ML estimators, respectively.

In addition to jackknife and bootstrap estimators of the variance of ρ_g , we calculated parametric estimates of variances of MANOVA estimates of ρ_g using the estimators described by Scheinberg (1966) and Falconer (1981). The estimator described by Scheinberg (1966) is

$$\hat{\sigma}_{S}^{2} = 32\hat{\rho}_{g}^{2}/r^{2} \left[(MS_{ga}^{2}/df_{g} + MS_{ea}^{2}/df_{e})/(4\hat{\sigma}_{ga}^{4}) + (MS_{gb}^{2}/df_{g} + MS_{eb}^{2}/df_{e})/(4\hat{\sigma}_{gb}^{4}) + (MS_{ga}MS_{gb} + MS_{gab}^{2})/(2df_{g}\hat{\sigma}_{gab}^{2}) - (MS_{ga}MS_{gab}/df_{g} + MS_{ea}MS_{eab}/df_{e})/(\hat{\sigma}_{ga}^{2}\hat{\sigma}_{gab}) - (MS_{gb}MS_{gab}/df_{g} + MS_{eb}MS_{eab}/df_{e})/(\hat{\sigma}_{gb}^{2}\hat{\sigma}_{gab}) + (MS_{gab}^{2}/df_{g} + MS_{eb}^{2}/df_{e})/(2\hat{\sigma}_{ga}^{2}\hat{\sigma}_{gb}^{2}) \right]$$
(6)

where df, and df, are the MANOVA degrees of freedom for

genotypes and error, respectively. The estimator described by Falconer is

$$\hat{\sigma}_{\rm F}^{\ 2} = \left[(1.0 - \hat{\rho}_{\rm g}^{\ 2})^2 \hat{\sigma}_{\rm Ha} \hat{\sigma}_{\rm Hb} / (2H_{\rm a}H_{\rm b}) \right]^2$$
(7)
where $\hat{\sigma}_{\rm Ha}^{\ 2} = 8H_{\rm a} / (nr)$ and $\hat{\sigma}_{\rm Hb}^{\ 2} = 8H_{\rm b} / (nr)$ are the estimates of
the variance of $H_{\rm a}$ and $H_{\rm b}$, respectively.

Simulation methods: Data were simulated for model (1) using factorial combinations of ρ_g , ρ_e , H_a , H_b , n, and r (Table 1.1). Although we assumed the properties of estimators of ρ_g were not affected by the sign of ρ_g , both negative and positive values of ρ_g were tested. We found the sign had no effect; thus, probabilities, biases, and variances estimated using the negative range of ρ_g are not reported. However, the response surfaces we report were estimated using the entire set of original values (Table 1.1). Two replications of 1000 data sets were simulated.

[Table 1.1 placement]

Data were simulated by setting $\sigma_{ea}^{\ 2} = \sigma_{eb}^{\ 2} = 1.0$ and using the equalities

 $\sigma_{eab} = \rho_{e} (\sigma_{ea}\sigma_{eb}) = \rho_{e},$ $\sigma_{ga}^{2} = H_{a} / [r(1.0 - H_{a})],$ $\sigma_{gb}^{2} = H_{b} / [r(1.0 - H_{b})],$

and $\sigma_{gab} = \rho_{g} (\sigma_{ga}\sigma_{gb})$

to define the variance-covariance matrices. These matrices were used to generate random vectors for G_{ai} , G_{bi} , ϵ_{aij} , and ϵ_{bij} . Simulations were done using a Floating Point System supercomputer (FPS-264S). The programs used were written in FORTRAN-77. Subroutines from the FPS FORTRAN library were used. Uniform random numbers were generated using the RAN function from the FPS-M64 library. Univariate normal deviates were generated using the algorithm of Kinderman (1975) and the uniform random numbers generated by the RAN function. Multivariate normal deviates were generated using the algorithm described by Johnson (1987).

MANOVA, ML, and REML methods were used to estimate ρ_g for each simulated data set. In addition, we used jackknifing and bootstrapping of MANOVA and ML estimators to estimate ρ_g . The biases and variances of these estimators were estimated from the simulated data. Biases and empirical variances $(\hat{\sigma}_{\rho}^{2})$ were estimated using

bias = $\bar{\rho}_{g} - \rho_{g}$

and

 $\hat{\sigma}_{\rho}^{2} = \Sigma (\hat{\rho}_{g} - \bar{\rho}_{g})^{2} / (s - 1), \qquad (8)$

respectively, where s is number of simulated experiments, $\bar{\rho}_{g}$ = s⁻¹ $\Sigma \hat{\rho}_{g}$ is the mean of simulated estimates, and ρ_{g} is the parametric or true value.

Results

Probabilities of non-positive definite variancecovariance matrices: The joint probabilities of negative MANOVA estimates of $\hat{\sigma}_{ga}^2$ or $\hat{\sigma}_{gb}^2$, $\Pr[\hat{\sigma}_{ga}^2 < 0 \text{ or } \hat{\sigma}_{gb}^2 < 0]$, ranged from 0.0 to 0.40 (Table 1.2). Probabilities of negative estimates were significantly decreased by increasing heritability and sample size, but were not affected by ρ_g and ρ_e (Tables 1.2 and 1.3). The main and interaction effects of heritability, n, and r were significant (Table 1.3). The main effect of the number of replications was substantially greater than the main effect of number of genotypes (Table 1.2).

> [Table 1.2 Placement] [Table 1.3 Placement] [Table 1.4 Placement] [Table 1.5 Placement]

The probabilities of MANOVA estimates of ρ_g greater than 1.0 or less than -1.0 ranged from 0.0 to 0.089 (Table 1.4). The maximum sum of probabilities of $\hat{\rho}_g > 1.0$ and $\hat{\rho}_g < -1.0$ was 0.099. Unlike the probabilities of negative estimates, these probabilities were significantly affected by ρ_g and ρ_e , in addition to being significantly affected by heritability, n, and r (Table 1.5). The effects of ρ_g , ρ_e , and heritability were greater than those of n and r. The probabilities of ρ_g less than -1.0 decreased as ρ_g increased, whereas the probabilities of ρ_g greater than 1.0 increased as $\rho_{\rm g}$ increased (Table 1.5). We estimated these probabilities separately because the probabilities were affected by the sign of $\rho_{\rm g}$ (Table 1.5). When n = 20, r = 6, H_a = 0.1, H_b = 0.9, and $\rho_{\rm g}$ = 0.9, for example, $\Pr[\hat{\rho}_{\rm g} < -1.0] = 0.0$ whereas $\Pr[\hat{\rho}_{\rm g} > 1.0] = 0.052$ (Table 1.4). Increasing heritability, n, and r decreases these probabilities.

Hill and Thompson (1978) estimated the probabilities of NPD MANOVA estimates of $\hat{\Sigma}_{g}$ for $\rho_{g} = 0$. We estimated the component probabilities of this probability for $\rho_{g} \neq 0.0$ (Tables 1.2 & 1.4); however, the sum of the probabilities we estimated are estimates of NPD estimates of $\hat{\Sigma}_{g}$. Hill and Thompson (1978) showed the probabilities of non-positive definite covariance matrices can be great when ρ_{g} is high "even when neither of the heritabilities is small"; however, we found this probability is zero or near zero when H_a and H_b are greater than or equal to 0.5 regardless of the values of n, r, ρ_{g} , and ρ_{e} (Tables 1.2 & 1.4).

These data show the probabilities of non-positive definite MANOVA estimates of the variance-covariance matrix are mainly a function of negative ANOVA estimates of variances. This problem is completely alleviated by using ML or REML estimation because negative estimates and estimates outside the parameter space do not arise using these methods (Amemiya 1985, Rao and Kleffe 1988, p233 - 256).

Empirical distribution of $\hat{\rho}_{g}$: MANOVA estimates of ρ_{g} were approximately normally distributed regardless of the

parameter values used (Figures 1 - 6). ML estimates were approximately normally distributed when $\rho_g = 0.1$ and H_a and H_b were greater or equal to 0.5 (Figures 4 and 5). Distributions of REML estimates were equivalent to those for ML estimates, so they are not shown. ML estimates were positively or negatively skewed depending on the value of ρ_g , e.g., the distributions for $\rho_g = 0.9$ are negatively skewed (Figures 3 and 6), whereas those for $\rho_g = -0.9$ were positively skewed mirror images of the distributions for $\rho_g = 0.9$.

[Figure 1, 2, 3, 4, 5, and 6 Placement] The distributions of MANOVA estimates illustrate the estimates outside the parameter space, but these distributions do not show the affect of negative estimates of variances because $\hat{\rho}_{g}$ is not defined when $\hat{\sigma}_{ga}^{2}$ or $\hat{\sigma}_{gb}^{2}$ is negative. ML and REML estimates yield estimates within the parameter space.

Biases of MANOVA, ML, REML, jackknife MANOVA and ML, and bootstrap MANOVA and ML estimates of ρ_g : MANOVA biases were significantly affected by ρ_g , ρ_e , H_a , H_b , n, and r. ML biases were significantly affected by ρ_g , H_a , H_b , n, and r. REML biases were significantly affected by ρ_g , ρ_e , H_a , H_b , and r. (Table 1.6). Biases of MANOVA, ML, and REML estimates were within ±0.02 and were not statistically significant when H_a and H_b were greater than or equal 0.5. MANOVA estimates of $\rho_g = 0.9$ were significantly over estimated (bias > 0), however, most of the ML and REML estimates of $\rho_g = 0.9$ were significantly under estimated (Table 1.7). Biases of MANOVA, ML, and REML estimates decreased and became less different as values of H_a , H_b , n, and r increased (Table 1.7). ML or REML estimation solves the problem of NPD estimates of $\hat{\Sigma}_g$; however, ML and REML estimates are biased.

> [Table 1.6 Placement] [Table 1.7 Placement] [Table 1.8 Placement]

Biases of jackknife MANOVA estimates were greater than MANOVA estimates, but biases of jackknife ML estimates were similar to ML estimates (Tables 1.7 and 1.8). Biases of bootstrap MANOVA and ML estimates were greater than MANOVA and ML estimates, respectively (Tables 1.7 and 1.8). Biases of bootstrap estimates for b = 100 were very close to those for b = 500 (Table 1.8).

Variances of estimators of ρ_{g} : Response surface analysis of empirical variances $(\hat{\sigma}_{\rho}^{2})$ (8) of MANOVA and ML estimates showed these variances were significantly affected by H_a, H_b, n, and r but not by ρ_{g} or ρ_{e} (Table 1.9). Variances of REML estimates were significantly affected by ρ_{g} , ρ_{e} , H_a, H_b, n, and r (Table 1.9).

> [Table 1.9 Placement] [Table 1.10 Placement] [Table 1.11 Placement]

The parametric variance estimator described by Scheinberg

(1966) $(\hat{\sigma}_{s}^{2})$ was substantially greater than the estimated variance of ρ_{g} $(\hat{\sigma}_{\rho}^{2})$ (Table 1.10). We found this estimator is not valid. The average estimate of Scheinberg variance was as great as 6.9 x 10¹⁰ when H_a and H_b were equal to 0.1. The parametric variance estimator decribed by and Falconer (1981) $(\hat{\sigma}_{F}^{2})$ was substantially greater than $\hat{\sigma}_{\rho}^{2}$ when one of the heritabilities was less than 0.5, but it is fearly close to $\hat{\sigma}_{\rho}^{2}$ when heritabilities were 0.5 or larger and the sample size is large (Table 1.10).

Jackknife variances of ML estimates were greater than estimated variances when H_a or H_b was less than 0.5, whereas bootstrap variances were fairly close to estimated variances (Table 1.11). Jackknife and bootstrap variances were very close to estimated variances when H_a and H_b were greater than or equal to 0.5 (Table 1.11). Variances of bootstrap estimates for b = 100 were very close to those of b = 500.

Estimated variances of ML estimates were very close to those of REML estimates (Table 1.11). Variances of MANOVA estimates were greater than those of ML and REML estimates (Table 1.10 and 1.11). Variances of MANOVA, ML, and REML decreased and became less different as H_a , H_b , n, and r increased (Table 1.10 and 1.11).

Discussion

The problem of NPD estimates of $\hat{\Sigma}_{g}$ using MANOVA methods can be alleviated by using ML or REML methods; however, the use of these methods is impractical because software has not been developed for linear models more complex than (1). As we stated earlier, the algorithms we implemented (Amemiya 1985; Klotz and Putter 1969) strictly apply to model (1); however, we expect computing solutions will ultimately be developed for linear models of arbitrary complexity.

Hill and Thompson (1978) showed, for $\rho_g = 0.0$, the probability of NPD estimates of $\hat{\Sigma}_g$ decreased as n and r increased, with r having a greater effect than n. We observed this for $\rho_g \neq 0.0$. The effect of r was rather pronounced, so the probability of NPD estimates of $\hat{\Sigma}_g$ can be decreased in practice by increasing the number of replications; however, this must usually be done at the expense of the number of genotypes (n). The costs of r and n are equal. Because the variance of ρ_g is more efficiently decreased by increasing n, as opposed to r, increasing r is contraindicated by the need for minimizing the variance of ρ_g .

We have shown MANOVA, ML, and REML estimates of ρ_g are biased (Table 1.7). The biases of ML and REML estimates are greater than the biases of MANOVA estimates when n and r are small, e.g., n = 20 and r = 3. Bias differences between these methods diminish as n and r increase. The bias of MANOVA estimates of ρ_g arise are explained by inequalities between expectations of ratios and ratios of expectations and expectations of products and products of expectations (Ponzoni and James 1978) and undefined estimates of ρ_g caused by negative estimates of the variances of ρ_g . We broke the probability of NPD estimates of $\hat{\Sigma}_g$ into its component parts to have an estimate of the number of undefined estimates of ρ_g . The absolute value of the bias of MANOVA estimates and probability of negative estimates are positively correlated and decrease as heritability, n, and r increase.

Bootstrapping and jackknifing were not effective for estimating bias and bias-corrected estimates of ρ_g . The degree of freedom bias correction used by Swallow and Monahan (1984) for estimating bias-corrected ML estimates of variances reduces bias for very small n, but has practically no effect when n is large. Besides, this correction, (n -1)/n, has no effect when applied to the variances and covariance of $\hat{\rho}_g$ because bias corrections applied to the numerator and denominator of $\hat{\rho}_g$ cancel, i.e., $\hat{\rho}_g = [(n 1)/n]\hat{\sigma}_{gab} / {[(n - 1)/n]\hat{\sigma}_{ga}^2[(n - 1)/n]\hat{\sigma}_{gb}^2}^{\frac{1}{2}} = \hat{\sigma}_{gab} /$ $(\hat{\sigma}_{ga}^2 \hat{\sigma}_{gb}^2)^{\frac{1}{2}}$. The variances of MANOVA, ML, or REML estimates of ρ_g are significantly greater than the biases of ρ_g , so bias is a comparatively minor problem.

We found parametric estimators of the variance of ρ_g (Scheinberg 1966; Falconer 1981) are not valid. These estimators overestimate the variance of ρ_g and are grossly inadequate when either of the heritabilities is less than 0.5. In addition, the variance of ρ_g was overestimated by the jackknife estimators. Unlike the other estimators, the bootstrap estimators, bootstrapping either MANOVA, ML, or REML estimators, gave valid estimates of the variance of ρ_g , i.e., estimates which are not significantly different from the empirically estimated variances of ρ_g . Bootstrap estimators of the variance of ρ_g fill the need for a valid estimator of this parameter. We found no significant difference between using b = 100 or b = 500 bootstrap samples; however, b = 500 may be needed to get valid interval estimates using bootstrapping, a subject we address elsewhere.

The variances of MANOVA estimators of the variance of ρ_g are greater than variances of ML or REML estimators; thus, even though these estimators are biased, their use is justified. The variance of ρ_g is efficiently decreased by increasing the number of genotypes, but not by increasing the number of replications of genotypes. The latter does not affect the degrees of freedom for genotypes. This finding is consistent with findings for variances. The variances of variances are minimized by maximizing n.

This study leads us to encourage the use of ML or REML estimators of ρ_g , bootstrap ML or REML estimators of the variance of ρ_g , and a maximum number of genotypes at the expense of replications of genotypes. The unbalanced designs developed for optimizing variance estimation should be equally optimal for estimating ρ_g . Finally, there is a great need for software for estimating Σ_g using ML or REML methods for linear models more complex than (1).

ACKNOWLEDGEMENTS

Our research was partially supported by a grant from Pioneer Hi-Bred International, Inc. Computing costs were covered by the College of Agricultural Sciences and the Agricultural Experiment Station.

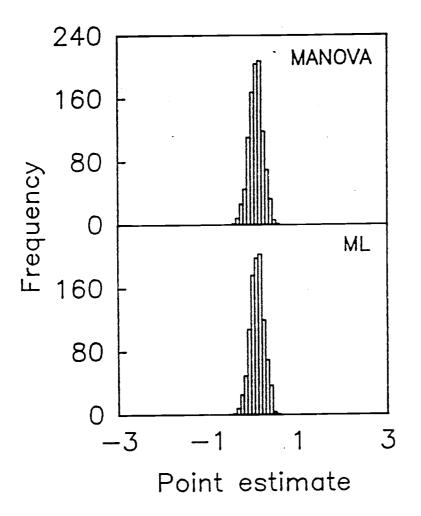


Figure 1. Frequency distributions of MANOVA and ML estimates of ρ_g when $\rho_g = 0.1$, $\rho_e = 0.1$, $H_a = 0.5$, $H_b = 0.5$, n = 60, and r = 6.

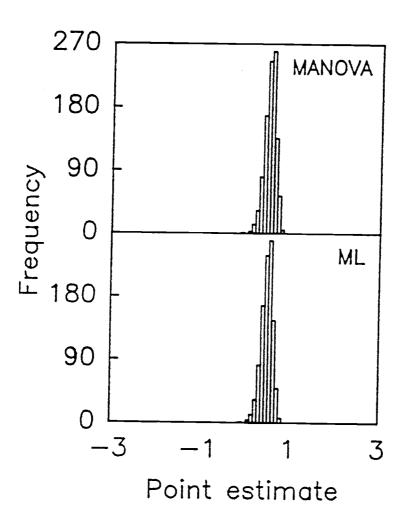


Figure 2. Frequency distributions of MANOVA and ML estimates of ρ_g when $\rho_g = 0.5$, $\rho_e = 0.1$, $H_a = 0.5$, $H_b = 0.5$, n = 60, and r = 6.

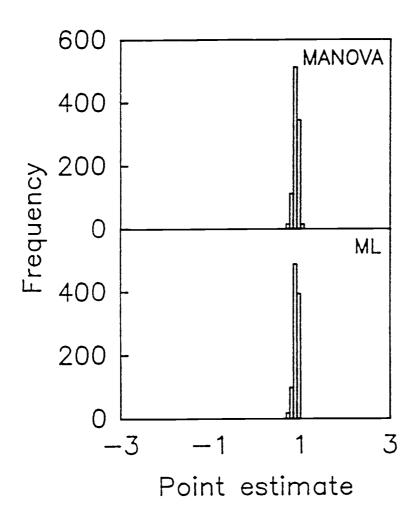


Figure 3. Frequency distributions of MANOVA and ML estimates of ρ_g when $\rho_g = 0.9$, $\rho_e = 0.1$, $H_a = 0.5$, $H_b = 0.5$, n = 60, and r = 6.

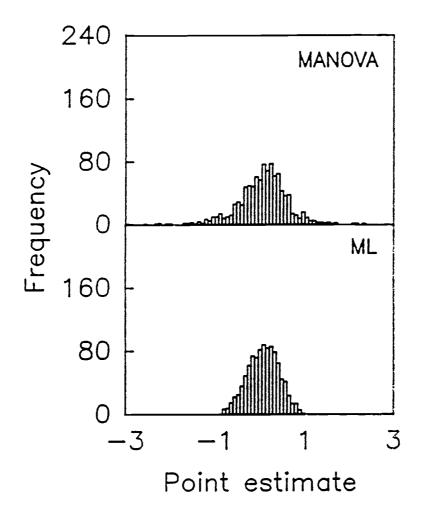


Figure 4. Frequency distributions of MANOVA and ML estimates of ρ_g when $\rho_g = 0.1$, $\rho_e = 0.1$, $H_a = 0.1$, $H_b = 0.1$, n = 60, and r = 6.

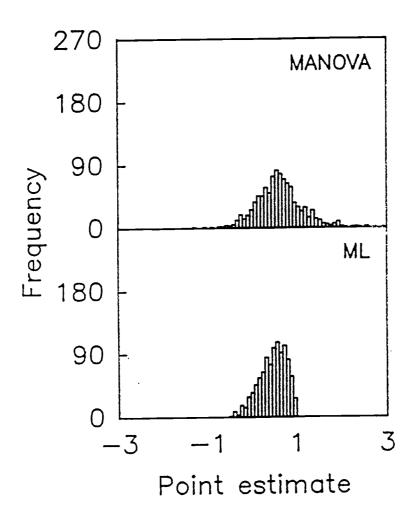


Figure 5. Frequency distributions of MANOVA and ML estimates of ρ_g when $\rho_g = 0.5$, $\rho_e = 0.1$, $H_a = 0.1$, $H_b = 0.1$, n = 60, and r = 6.

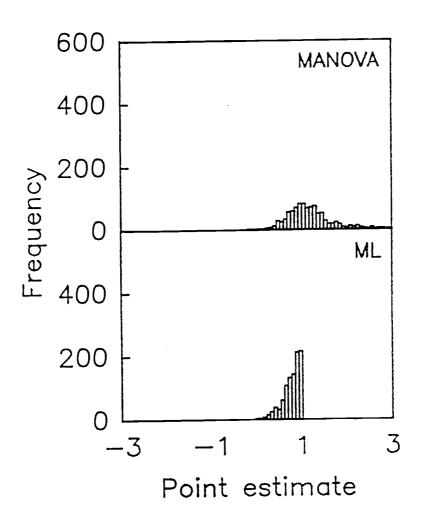


Figure 6. Frequency distributions of MANOVA and ML estimates of ρ_g when $\rho_g = 0.9$, $\rho_e = 0.1$, $H_a = 0.1$, $H_b = 0.1$, n = 60, and r = 6.

Parameter	Assigned value			
Genetic correlation (ρ_g)	-0.9, -0.5, -0.1, 0.1, 0.5, 0.9			
Environmental correlation (ρ_{e})	0.1, 0.5, 0.9			
Heritabilities of two traits (H _a , H _b)	(0.1,0.1), (0.1,0.5),(0.1,0.9) (0.5,0.5), (0.5,0.9), (0.9,0.9)			
Number of genotypes (n)	20, 60, 100			
Number of replications (r)	3, 6, 9			

Table 1.1 Parameters and their assigned values used in the simulation.

Table 1.2 Probabilities of negative MANOVA estimates of genetic variances $Pr(\hat{\sigma}_{ga}^2 < 0 \text{ or } \hat{\sigma}_{gb}^2 < 0)$ for different values of H_a , H_b , n, and r. The probabilities were averages over the values of ρ_g and ρ_e used.

			r			
H _a	H _b	n	3	6	9	
0.1	0.1	20	0.402	0.185	0.077	
		60	0.195	0.017	0.001	
		100	0.095	0.002	0.000	
	0.5	20	0.255	0.103	0.043	
		60	0.110	0.008	0.000	
		100	0.055	0.001	0.000	
	0.9	20	0.252	0.107	0.042	
		60	0.111	0.010	0.001	
		100	0.055	0.001	0.000	
0.5	0.5	20	0.002	0.000	0.000	
		60	0.000	0.000	0.000	
		100	0.000	0.000	0.000	
	0.9	20	0.001	0.000	0.000	
		60	0.000	0.000	0.000	
		100	0.000	0.000	0.000	
0.9	0.9	20	0.000	0.000	0.000	
		60	0.000	0.000	0.000	
		100	0.000	0.000	0.000	

Table 1.3 Response surface analysis where the probability of negative estimates of $\hat{\sigma}_{ga}^2$ or $\hat{\sigma}_{gb}^2$ is the dependent variable, ρ_g , ρ_e , H_a , H_b , n, and r as are independent variables, and $\hat{\sigma}_{ga}^2$ or $\hat{\sigma}_{gb}^2$ were estimated using MANOVA. b_i is the regression coefficient for the ith main or interaction effect.

Parameter	b <u>i</u>	P-value
Intercept	709.86	< 0.01
ρ _g	-9.86	0.60
ρ _e	-30.08	0.11
Ha	-595.22	< 0.01
H _b	-347.45	< 0.01
n	-5.06	< 0.01
r	-75.45	< 0.01
$\rho_{g} \propto \rho_{g}$	1.70	0.90
$\rho_{g} \propto \rho_{e}$	-4.41	0.65
$\rho_{e} \propto \rho_{e}$	-6.13	0.65
$H_a \propto \rho_g$	-0.74	0.95
$H_a \propto \rho_e$	0.78	0.95
$H_a \propto H_a$	201.40	< 0.01
$H_b \propto \rho_g$	8.86	0.47
$H_b \propto \rho_e$	25.89	0.03
H _b x H _a	-4.32	0.89
H _b x H _b	140.58	< 0.01
$n \ge \rho_g$	0.02	0.75
$n \ge \rho_e$	0.13	0.17
пхН _а	2.15	< 0.01
пхН _ь	0.92	< 0.01
nxn	0.01	< 0.01
$r \ge \rho_g$	0.33	0.80
$r \times \rho_e$	1.55	0.22
гхН _а	31.24	< 0.01
r x H _b	13.28	< 0.01
rxn	0.18	< 0.01
rxr	2.55	< 0.01

Table 1.4 Probabilities of estimates of $\hat{\rho}_{g}$ out of the parameter space, $\Pr(\hat{\rho}_{g} > 1.0)$ and $\Pr(\hat{\rho}_{g} < -1.0)$, estimated using MANOVA and different values of H_a, H_b, ρ_{g} , n, and r. The probabilities were the average over values of ρ_{e} used.

H _a 0.1	Н _ь	ρ _g 0.1 0.5	n 20 60 100 20	< -1.0 0.047 0.038 0.032	3 > 1.0 0.030 0.008	< -1.0	6 > 1.0 0.009	< -1.0	9 > 1.0
		0.1	20 60 100 20	0.047	0.030	0.037			> 1.0
0.1	0.1		60 100 20	0.038			0.009		
			60 100 20	0.038				11 11/4	0.004
		0.5	100 20			0.012	0.001	0.002	0.000
		0.5	20		0.005	0.003	0.000	0.000	0.000
				0.022	0.059	0.014	0.024	0.008	0.008
			60	0.013	0.022	0.002	0.002	0.000	0.000
			100	0.008	0.014	0.000	0.000	0.000	0.000
		0.9	20	0.010	0.089	0.001	0.055	0.001	0.025
			60	0.002	0.068	0.000	0.014	0.000	0.002
			100	0.000	0.047	0.000	0.003	0.000	0.000
(0.5	0.1	20	0.015	0.008	0.005	0.002	0.003	0.001
			60	0.003	0.003	0.000	0.000	0.000	0.000
			100	0.002	0.001	0.000	0.000	0.000	0.000
		0.5	20	0.005	0.022	0.001	0.009	0.000	0.004
			60	0.000	0.010	0.000	0.001	0.000	0.000
			100	0.000	0.009	0.000	0.000	0.000	0.000
		0.9	20	0.000	0.049	0.000	0.034	0.000	0.014
			60	0.000	0.039	0.000	0.010	0.000	0.000
			100	0.000	0.027	0.000	0.002	0.000	0.000
(0.9	0.1	20	0.007	0.008	0.002	0.003	0.001	0.001
			60	0.002	0.003	0.000	0.000	0.000	0.000
			100	0.000	0.000	0.000	0.000	0.000	0.000
		0.5	20	0.001	0.019	0.000	0.011	0.000	0.005
			60	0.000	0.014	0.000	0.002	0.000	0.000
			100	0.000	0.010	0.000	0.000	0.000	0.000
		0.9	20	0.000	0.052	0.000	0.039	0.000	0.020
			60	0.000	0.041	0.000	0.010	0.000	0.001
			100	0.000	0.036	0.000	0.002	0.000	0.000

Table 1.4 continued

							r		
					3		6		9
Ha	H _b	ρ _g	n	< -1.0	> 1.0	< -1.0	> 1.0	< -1.0	> 1.0
0.5	0.5	0.1	20 60	0.000	0.000	0.000 0.000	0.000	0.000 0.000	0.000
		0.5	100 20 60	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000
		0.9	100 20 60	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000
			100	0.000	0.000	0.000	0.000	0.000	0.000
	0.9	0.1	20 60 100	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000	0.000	0.000
		0.5	20 60	0.000 0.000	0.000 0.000	0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000
		0.9	100 20 60	0.000 0.000 0.000	0.000 0.001 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000
			100	0.000	0.000	0.000	0.000	0.000	0.000
0.9	0.9	0.1	20 60	0.000	0.000	0.000	0.000	0.000 0.000	0.000
		0.5	100 20 60	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000
		0.9	100 20 60	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000 0.000	0.000 0.000
			100	0.000	0.000	0.000	0.000	0.000	0.000 0.000

Table 1.5 Response surface analysis where the probability of estimates of $\hat{\rho}_{g}$ outside the parameter space $[\Pr(\hat{\rho}_{g} < -1.0) \text{ and } \Pr(\hat{\rho}_{g} > 1.0)]$ is the dependent variable, ρ_{g} , ρ_{e} , H_{a} , H_{b} , n, and r are the independent variables, and $\hat{\rho}_{g}$ is estimated using MANOVA. b_{i} is the regression coefficient for the ith main or interaction effect.

	ρ _g < -1	.0	$\hat{\rho}_{g} > 1.0$		
Parameter	b _i	P-value	b _i	P-value	
Intercept	54.52	< 0.01	88.46	< 0.01	
ρ _g	-13.72	< 0.01	64.37	< 0.01	
ρ _e	-70.26	< 0.01	-83.89	< 0.01	
Ha	-36.62	< 0.01	-57.28	< 0.01	
н _ь	-9.91	< 0.01	-59.99	< 0.01	
n	-0.28	< 0.01	-0.54	< 0.01	
r	-4.08	< 0.01	-9.29	< 0.01	
ρ _g χ ρ _g	2.01	0.45	32.79	< 0.01	
$\rho_{g} \propto \rho_{e}$	5.25	0.22	-7.37	0.44	
ραχρ	25.77	< 0.01	32.08	< 0.01	
$H_a \propto \rho_g$	4.16	0.01	-37.33	< 0.01	
$H_a \times \rho_e$	23.26	< 0.01	-7.95	0.03	
HaxHa	5.68	< 0.01	15.94	< 0.01	
$H_b \propto \rho_g$	-1.61	0.33	7.82	0.03	
$H_{b} \times \rho_{e}$	-7.19	< 0.01	40.19	< 0.01	
H _b x H _a	-5.86	< 0.01	-14.99	< 0.01	
H _b x H _b	0.39	0.83	4.25	0.30	
n x ρ _R	0.04	0.01	0.22	< 0.01	
n x $ ho_{e}$	0.15	< 0.01	0.17	< 0.01	
n x H _a	0.08	< 0.01	-0.17	< 0.01	
n x H _b	-4.0 x 10 ⁻⁵	0.99	0.15	< 0.01	
nxn	0.01	< 0.01	0.01	< 0.01	
r x ρ _g	0.41	0.06	4.32	< 0.01	
r x ρ_{e}	2.39	< 0.01	2.69	< 0.01	
r x H _a	1.23	< 0.01	-3.77	< 0.01	
r x H _b	-0.07	0.66	2.70	< 0.01	
rxn	0.01	0.06	0.01	< 0.01	
rxr	0.09	< 0.01	0.32	< 0.01	

Table 1.6 Response surface analysis where biases of MANOVA, ML, and REML estimators of $\rho_{\rm g}$ are the dependent variables and $\rho_{\rm g}$, $\rho_{\rm e}$, $\rm H_{a}$, $\rm H_{b}$, n, and r are the independent variables. $\rm b_{i}$ is the regression coefficient for the ith main or interaction effect.

	MA	NOVA	M	L		REML
Parameter	b _i I	?-value	b _i	P-value	b _i	P-value
Intercept	0.0328	0.05	-0.1556	< 0.01	0.0374	0.05
ρ _g	0.3060	< 0.01	-0.2873	< 0.01	-0.3562	< 0.01
ρ _e	-0.2821	< 0.01	0.0138	0.46	0.2170	< 0.01
Ha	-0.1089	< 0.01	0.2345	< 0.01	-0.1711	< 0.01
H _b	0.1005	< 0.01	0.1092	< 0.01	0.2830	< 0.01
n	-0.0005	0.01	0.0013	< 0.01	-0.0003	0.15
r	-0.0095	0.01	0.0226	< 0.01	-0.0086	0.04
ρ _g χρ _g	0.0278	0.05	-0.0299	0.02	-0.0341	0.03
$\rho_{g} \propto \rho_{e}$	0.0125	0.21	0.0475	< 0.01	0.0479	< 0.01
$\rho_{e} \propto \rho_{e}$	0.0060	0.69	-0.0086	0.53	-0.0363	0.04
$H_a \propto \rho_g$	-0.1639	< 0.01	0.1136	< 0.01	0.1307	< 0.01
$H_a \propto \rho_e$	0.0327	0.01	0.0012	0.92	-0.0753	< 0.01
H _a x H _a	0.1044	< 0.01	-0.0798	< 0.01	0.0917	< 0.01
$H_b \propto \rho_g$	-0.1346	< 0.01	0.0368	< 0.01	0.0686	< 0.01
$H_b \times \rho_e$	0.2256	< 0.01	0.0056	0.64	-0.0206	0.19
H _b x H _a	-0.0744	0.03	-0.0207	0.51	-0.0800	0.05
H _b x H _b	-0.0758	< 0.01	-0.0713	< 0.01	-0.1081	< 0.01
$\tilde{n x \rho_g}$	-0.0006	< 0.01	0.0012	< 0.01	0.0014	< 0.01
nχρ _e	0.0004	< 0.01	-0.0002	0.02	-0.0008	< 0.01
n x Ha	0.0004	< 0.01	-0.0009	< 0.01	0.0007	< 0.01
n x H _b	8.1 x 10 ⁻⁶	0.95	4.0×10^{-5}	0.74	-0.0006	< 0.01
nxn	1.4 x 10 ⁻⁶		-5.4 x 10 ⁻⁵	< 0.01	1.0 x 10	
r x ρ _g	-0.0121	< 0.01	0.0182	< 0.01	0.0220	< 0.01
rxρ	0.0061	< 0.01	-0.0032	0.01	-0.0139	< 0.01
rхH _a	0.0081	< 0.01	-0.0147	< 0.01	0.0102	< 0.01
r x H _b	-0.0017	0.35	-0.0014	0.39	-0.0095	< 0.01
rxn	3.7×10^{-5}		-5.7 x 10 ⁻⁵		4.6 x 10	
rxr	0.0003	0.16	-0.0010	< 0.01	0.0004	0.16

	Estimation					1
Нъ	ρ_{g}	n	r	MANOVA	ML	REML
0.1	0.1	20	3	0.020	0.039*	0.176*
			6	-0.153	-0.027	0.018
			9	-0.140*	-0.062*	-0.044*
		60	3	-0.177*	-0.047*	0.032
			6	-0.108*	-0.060*	-0.055*
			9	-0.050*	-0.041*	-0.041*
		100	3	-0.167*	-0.067*	-0.035*
			6	-0.055*	-0.045*	-0.044*
			9	-0.019*	-0.019*	-0.019*
	0.5	20	3	0.104	-0.197*	-0.102*
			6	-0.004	-0.123*	-0.107*
			9	-0.025	-0.071*	-0.069*
		60	3	0.004	-0.130*	-0.080*
			6	-0.022	-0.036*	-0.035*
			9	-0.019*	-0.020*	-0.020*
		100	3	-0.025	-0.092*	-0.063*
			6	-0.017	-0.020*	-0.019*
			9	-0.004	-0.005	-0.005
	0.9	20	3	0.171*	-0.434*	-0.420*
			6	0.188*	-0.200*	-0.203*
			9	0.106*	-0.098*	-0.096*
		60	3	0.209*	-0.238*	-0.229*
			6	0.058*	-0.040*	-0.040*
			9	0.019*	-0.013*	-0.013*
		100	3	0.139*	-0.134*	-0.132*
			6	0.034*	-0.012*	-0.012*
			9	0.011*	-0.003	-0.003
0.5	0.1	20	3	-0.028	-0.029	0.167*
			6	-0.036	-0.034*	0.048*
			9	-0.031	-0.025*	0.003
		60	3	-0.022	-0.030*	0.069*
			6	-0.021*	-0.018*	-0.011
			9	-0.007	-0.007	-0.007
		100	3	-0.019	-0.025*	0.024*
			6	-0.011	-0.011	-0.008
			9	-0.006	-0.006	-0.006

Table 1.7 Biases^a of MANOVA, ML, and REML estimators of $\rho_{\rm g}$. The value of H_a was 0.1 in all cases.

				Estir	nation Metho	đ
H _b	ρ _g	n	r	MANOVA	ML	REML
	0.5	20	3	0.046	-0.163*	0.013
			6	0.037*	-0.048*	0.015
			9	0.020	-0.018	0.009
		60	3	0.049*	-0.046*	0.023
			6	0.023*	0.006	0.014*
			9	0.006	0.005	0.005
		100	3	0.058*	-0.007	0.031*
			6	0.006	0.005	0.005
			9	0.000	0.000	0.000
	0.9	20	3	0.119*	-0.318*	-0.166*
			6	0.128*	-0.129*	-0.074*
			9	0.080*	-0.052*	-0.028*
		60	3	0.140*	-0.137*	-0.080*
			6	0.061*	-0.006	-0.003
			9	0.020*	0.002	0.003
		100	3	0.120*	-0.069*	-0.045*
			6	0.028*	0.003	0.004
			9	0.008*	0.003	0.003
0.9	0.1	20	3	0.007	-0.031*	0.175*
			6	0.002	-0.010	0.086*
			9	-0.009	-0.015	0.024
		60	3	0.005	-0.010	0.095*
			6	0.000	-0.001	0.008
			9	-0.001	-0.001	-0.000
		100	3	0.005	-0.003	0.048*
			6	-0.001	-0.001	-0.000
			9	-0.000	-0.000	-0.000
	0.5	20	3	0.043	-0.160*	0.050*
			6	0.078*	-0.035*	0.055*
			9	0.036*	-0.011	0.026*
		60	3	0.079*	-0.040*	0.052*
			6	0.034*	0.014*	0.025*
			9	0.009	0.007	0.009
		100	3	0.077*	0.000	0.050*
			6	0.011*	0.009*	0.010*
			9	0.004	0.004	0.004

Table	1.7	continued.

				Estin	nation Method	1
Нъ	ρ_{g}	n	r	MANOVA	ML	REML
	0.9	20	3	0.107*	-0.321*	-0.131*
			6	0.146*	-0.130*	-0.039*
			9	0.110*	-0.046*	-0.011*
		60	3	0.156*	-0.138*	-0.054*
			6	0.070*	-0.014*	-0.004
			9	0.026*	0.002	0.002
		100	3	0.133*	-0.076*	-0.031*
			6	0.034*	0.002	0.002
			9	0.011*	0.004*	0.004*

^aAsterisks denote biases significantly different from 0.0 using a Type I probability of 0.05.

Table 1.8 Biases^a of jackknife and bootstrap estimates of ρ_g estimated using MANOVA and ML. The bootstrap sample sizes (b) used were 100 and 500. The value of H_a used was 0.1.

				Jackl	knife		Bootstrap			
						b = 1	100	b = !	500	
Η _b ρ	$ ho_{g}$	n	n	r	MANOVA	ML	MANOVA	ML	MANOVA	ML
0.1	0.1	20	3	-0.116	-0.023	0.011	-0.061*	0.099	-0.062*	
			6	-3.503*	-0.108*	-0.004	-0.047*	-0.134	-0.049*	
			9	-8.176*	-0.272*	-0.048	-0.021	-0.011	-0.023	
		60	3	1.250*	0.005	-0.125	-0.042*	0.075	-0.041*	
			6	-1.547*	0.101*	-0.015	-0.016	-0.016	-0.017	
			9	-6.023*	-0.053	-0.006	-0.009	-0.006	-0.010	
		100	3	0.806*	0.000	-0.023	-0.026	-0.044	-0.026	
			6	-0.851*	0.071*	-0.017	-0.017	-0.018	-0.017	
			9	-3.646*	0.029	-0.010	-0.010	-0.010	-0.010	
	0.5	20	3	3.928*	-0.399*	0.475*	-0.359*	0.449*	-0.359*	
			6	-6.843*	-0.281*	0.320*	-0.233*	0.369*	-0.233*	
			9	-23.416*	-0.210*	0.220*	-0.141*	0.207*	-0.141*	
		60	3	0.983*	-0.101*	0.346*	-0.222*	0.343*	-0.223*	
			6	-0.876*	0.084*	0.175*	-0.034*	0.178*	-0.033*	
			9	-7.559*	0.081*	0.082*	0.013	0.079*	0.013	
		100	3	0.146*	-0.016	0.276*	-0.140*	0.281*	-0.142*	
			6	-0.149*	0.001	0.092*	0.013	0.092*	0.013	
			9	-2.795*	0.016	0.033*	0.022*	0.032*	0.021*	
	0.9	20	3	5.282*	-0.130*	0.684*	-0.670*	0.778*	-0.670*	
			6	-6.060*	-0.128*	0.656*	-0.443*	0.735*	-0.442*	
			9	-28.198*	0.077	0.580*	-0.275*	0.581*	-0.276*	
		60	3	0.550*	0.001	0.649*	-0.452*	0.631*	-0.453*	
			6	-0.228*	-0.000	0.341*	-0.152*	0.360*	-0.153*	
			9	-6.635*	0.015	0.172*	-0.047*	0.174*	-0.047*	
		100	3	0.010	0.004	0.642*	-0.322*	0.650*	-0.323*	
			6	-0.053*	0.006	0.208*	-0.062*	0.206*	-0.061*	
			9	-2.263*	0.006	0.068*	-0.017*	0.068*	-0.018*	

				Jackl	knife	Bootstrap				
						b = 1	100	b = 500		
Hb	$ ho_{g}$	n	r	MANOVA	ML	MANOVA	ML	MANOVA	ML	
0.5	0.1	20	3	0.202*	-0.015	0.015	-0.054*	-0.033	-0.055*	
			6	-1.515*	0.050	0.110*	-0.027*	0.024	-0.028*	
			9	-4.318*	-0.172*	0.007	-0.013	-0.001	-0.013	
		60	3	-0.021	0.004	0.004	-0.023*	0.008	-0.024*	
			6	-0.867*	0.031	0.012	-0.003	0.008	-0.004	
			9	-3.269*	-0.013	0.006	0.004	0.006	0.003	
		100	3	0.027	-0.014	0.023	-0.008	0.020	-0.009	
			6	-0.454*	0.054*	0.000	-0.002	0.001	-0.003	
			9	-1.976*	0.127*	-0.003	-0.004	-0.003	-0.003	
	0.5	20	3	-0.025	0.060	0.210*	-0.237*	0.239*	-0.236*	
			6	-2.764*	-0.266*	0.171*	-0.114*	0.185*	-0.113*	
			9	-10.757*	0.085*	0.145*	-0.057*	0.140*	-0.056*	
		60	3	-0.046	0.016	0.161*	-0.101*	0.167*	-0.102*	
			6	-0.622*	0.023	0.096*	0.004	0.099*	0.004	
			9	-4.565*	0.056*	0.044*	0.021*	0.045*	0.022*	
		100	3	-0.013	0.042*	0.142*	-0.045*	0.141*	-0.045*	
			6	-0.085*	-0.005	0.052*	0.023*	0.051*	0.023*	
			9	-1.374*	0.013*	0.016	0.012*	0.016*	0.012*	
	0.9	20	3	-0.063	-0.040	0.456*	-0.457*	0.500*	-0.456*	
			6	-3.545*	0.139*	0.375*	-0.251*	0.358*	-0.252*	
			9	-16.002*	-0.032	0.277*	-0.155*	0.278*	-0.154*	
		60	3	-0.003	0.027*	0.339*	-0.248*	0.326*	-0.248*	
			6	-0.200*	-0.017*	0.167*	-0.062*	0.169*	-0.063*	
			9	-2.912*	0.006	0.090*	-0.011*	0.089*	-0.011*	
		100	3	-0.003	-0.002	0.299*	-0.160*	0.295*	-0.161*	
			6	-0.000	-0.000	0.091*	-0.018*	0.093*	-0.018*	
			9	-0.775*	0.006*	0.043*	0.004	0.043*	0.004	

				Jack	knife		Boots	trap	
						b = 1	100	b = !	500
H _b	$ ho_{g}$	n	r	MANOVA	ML	MANOVA	ML	MANOVA	ML
0.9	0.1	20	3	-0.212*	-0.005	0.025	-0.041*	0.032	-0.039*
			6	-1.584*	-0.053	0.061	-0.007	0.062	-0.006
			9	-4.060*	-0.135*	0.026	-0.008	0.019	-0.008
		60	3	0.058	0.005	0.030	-0.024*	0.031	-0.025*
			6	-0.944*	0.039	0.029*	0.013	0.028*	0.013
			9	-3.296*	0.081*	0.005	0.002	0.005	0.002
		100	3	-0.092*	0.030	0.022	-0.009	0.026	-0.009
			6	-0.540*	0.076*	0.008	0.004	0.008	0.003
			9	-2.186*	0.047*	0.008	0.008	0.009	0.008
	0.5	20	3	-0.207*	-0.049	0.159*	-0.235*	0.160*	-0.236*
			6	-3.446*	0.115*	0.185*	-0.108*	0.201*	-0.109*
			9	-11.152*	-0.058	0.135*	-0.048*	0.143*	-0.048*
		60	3	-0.087*	0.009	0.197*	-0.102*	0.185*	-0.103*
			6	-0.616*	0.038*	0.092	0.008	0.088*	0.008
			9	-4.674*	0.069*	0.039*	0.018*	0.040*	0.018*
		100	3	-0.003	0.005	0.158*	-0.038*	0.174*	-0.037*
			6	-0.045*	0.004	0.056*	0.025*	0.054*	0.025*
			9	-1.531*	0.013*	0.017*	0.014*	0.017*	0.014*
	0.9	20	3	-0.437*	0.228*	0.381*	-0.439*	0.405*	-0.440*
			6	-3.661*	0.084*	0.316*	-0.256*	0.351*	-0.256*
			9	-14.727*	-0.055	0.284*	-0.151*	0.280*	-0.151*
		60	3	-0.023*	-0.000	0.322*	-0.248*	0.347*	-0.249*
			6	-0.097*	0.002	0.166*	-0.054*	0.168*	-0.054*
			9	-3.464*	-0.003	0.087*	-0.010*	0.085*	-0.010*
		100	3	-0.001	-0.000	0.284*	-0.153*	0.291*	-0.153*
			6	-0.006	-0.001	0.100*	-0.015*	0.101*	-0.015*
			9	-0.845*	0.004	0.039*	0.005*	0.039*	0.005*

^aAsterisks denote biases significantly different from 0.0 using a Type I probability of 0.05.

Table 1.9 Response surface analysis where the empirical variances $(\hat{\sigma}_{\rho}^{2})$ of MANOVA, ML, and REML estimates of $\hat{\rho}_{g}$ are the dependent variables and ρ_{g} , ρ_{e} , H_{a} , H_{b} , n and r are the independent variables. b_{i} is the regression coefficient for the ith main or interaction effect.

	1	MANOVA		ML	REML		
Parameter	b _i	P-valu	e b _i	P-value	b	P-value	
Intercept	7.97	< 0.01	0.66	< 0.01 0	.79	< 0.01	
ρ _g -0			-0.07	0.10 -0		< 0.01	
ρ_{e} -1		0.07			.11	< 0.01	
H _a -2		< 0.01			.76		
H _b - 10		< 0.01	-0.48		.26	< 0.01	
n -0			-4.2×10^{-3}	< 0.01 -5			
r -0	. 47	< 0.01			.06	< 0.01	
$\rho_{g} \ge \rho_{g} = 0$.14	0.73	-0.03		.01	0.35	
$\rho_{e} \propto \rho_{g} - 1$.14	0.01	-0.01	0.02 -0	.07		
$\rho_{e} \propto \rho_{e} = 1.$	08	0.02	6.0×10^{-4}		.06	< 0.01	
$H_a \propto \rho_g - 0$. 58		-0.01	0.27 0	.10	< 0.01	
	.03	0.94	3.1 x 10 ⁻³		.07	< 0.01	
$H_a \times H_a = 0.$		0.19	0.15	< 0.01 0	.22	< 0.01	
	73	< 0.01	0.07	< 0.01 0	.03	< 0.01	
$H_b \times \rho_e 0.$	18	0.66	0.01	0.13 -0	.05	< 0.01	
$H_b \times H_a = 0$.	05	0.95	0.07	< 0.01 0	.06	0.03	
$H_b \times H_b = 4$.		< 0.01	0.18	< 0.01 0	.13	< 0.01	
$n \ge \rho_g = 3.$	7 x 10 ⁻³	0.21	5.0×10^{-4}	< 0.01 1	$.1 \times 10^{-3}$	< 0.01	
$n \propto \rho_{e}$ 1.	8×10^{-3}	0.58	8.1 x 10 ⁻⁵		$.4 \times 10^{-4}$	< 0.01	
nxH _a 7.	2×10^{-3}	0.08	1.5 x 10 ⁻³	< 0.01 2	$.2 \times 10^{-3}$	< 0.01	
nxH _b 0.	03	< 0.01	7.0×10^{-4}	< 0.01 2	$.8 \times 10^{-4}$	0.01	
	$.0 \times 10^{-4}$		1.5×10^{-5}	< 0.01 1	$.7 \times 10^{-5}$	< 0.01	
$r \ge \rho_g - 0$.			-3.0×10^{-3}	< 0.01 0	.01	< 0.01	
$r \propto \rho_e = 0.$			3.0×10^{-4}	0.61 0	.01	< 0.01	
$r x H_a = 0.$		0.02	0.02	< 0.01 0	.03	< 0.01	
$r \times H_b = 0$.	31		0.02		.01	< 0.01	
			2.3×10^{-5}		$.1 \times 10^{-5}$		
rxr O	.01	0.39	1.2×10^{-3}		$.0 \times 10^{-3}$	< 0.01	

H _a						$\hat{\sigma}_{B}$	2		
	Н _ь	n	r	$\hat{\sigma}_{\rho}^{2}$	$\hat{\sigma}_{\mathrm{J}}^{2}$	b = 100	b = 500	$\hat{\sigma}_{\rm S}^{2}$	$\hat{\sigma}_{\rm F}^{\ 2}$
0.1	0.1	20	3	4.198	98.591	38.915	34.731	1.2 x 10 ⁶	5.4 x 10 ⁴
			6	4.535	37.987	13.023	20.849	2.9×10^9	7.1×10^{5}
			9	1.713	8.228	17.413	8.129	6.7×10^{7}	1.2×10^{6}
		60	3	3.207	172.287	27.953	65.729	6.4×10^8	3.0×10^{4}
			6	0.687	8.783	1.784	3.099	1.6 x 10 ⁵	2.7×10^4
			9	0.098	1.416	0.533	0.898	2.4 x 10	0.82
		100	3	1.553	100.559	7.585	11.579	6.4 x 10 ⁵	8.3×10^4
			6	0.106	1.610	1.008	0.685	3.9 x 10	1.30
			9	0.039	0.267	0.071	0.085	0.19	0.06
0.1	0.5	20	3	1.018	13.101	5.612	15.829	2.5 x 10 ⁵	1.3×10^3
			6	0.450	15.891	8.988	2.085	1.1 x 10 ⁵	9.24
			9	0.207	1.864	2.113	1.593	3.5×10^4	6.6 x 10
		60	3	0.451	25.083	2.943	8.171	4.2 x 10 ⁵	3.3 x 10
			6	0.101	17.897	0.412	0.572	5.2×10^3	0.41
			9	0.033	0.149	0.474	0.176	1.51	0.04
		100	3	0.530	883.827	1.948	1.096	4.6 x 10 ⁷	0.24
			6	0.029	0.551	0.142	0.279	1.91	0.04
			9	0.019	0.019	0.052	0.033	1.95	0.04
0.1	0.9	20	3	1.043	22.119	2.607	3.264	6.2 x 10 ⁸	7.0 x 10
			6	0.440	7.480	2.838	4.075	1.9×10^{5}	9.46
			9	0.279	6.360	3.016	1.922	1.4×10^{5}	7.07
		60	3	0.400	17.524	1.104	3.403	2.1×10^5	2.41
			6	0.109	2.552	1.141	0.500	2.0×10^{3}	0.05
			9	0.036	0.110	0.153	0.165	2.3 x 10	0.03
		100	3	0.340	76.397	1.265	3.247	8.6 x 10 ⁶	8.3×10^2
			6	0.030	0.274	0.267	0.207	5.77	0.03
			9	0.016	0.018	0.027	0.028	0.07	0.02

Table 1.10 Empirical $(\hat{\sigma}_{\rho}^{2})$, jackknife $(\hat{\sigma}_{J}^{2})$, bootstrap $(\hat{\sigma}_{B}^{2})$, Scheinberg $(\hat{\sigma}_{S}^{2})$, and Falconer $(\hat{\sigma}_{F}^{2})$ variances of MANOVA estimators of ρ_{g} .

						$\hat{\sigma}_{B}$	2		$\hat{\sigma}_{\rm F}^{2}$
Ha	Н _ь	n	r	$\hat{\sigma}_{ ho}^{2}$	$\hat{\sigma}_{\mathrm{J}}^{2}$	b = 100	b = 500	$\hat{\sigma}_{\rm S}^{2}$	
0.5	0.5	20	3	0.097	0.319	0.626	0.415	1.0×10^{3}	5.56
			6	0.054	0.053	0.130	0.107	0.43	0.08
			9	0.046	0.044	0.044	0.041	0.16	0.06
		60	3	0.023	0.021	0.020	0.020	0.09	0.06
			6	0.015	0.014	0.013	0.013	0.06	0.03
			9	0.014	0.012	0.011	0.011	0.05	0.02
		100	3	0.013	0.012	0.011	0.011	0.05	0.03
			6	0.009	0.008	0.007	0.007	0.04	0.02
			9	0.008	0.007	0.006	0.006	0.03	0.01
	0.9	20	3	0.060	0.105	0.176	0.160	3.29	0.12
			6	0.043	0.044	0.042	0.046	0.16	0.06
			9	0.040	0.039	0.034	0.035	0.15	0.04
		60	3	0.016	0.015	0.014	0.014	0.06	0.04
			6	0.014	0.012	0.011	0.011	0.05	0.02
			9	0.013	0.011	0.010	0.010	0.05	0.01
		100	3	0.009	0.008	0.008	0.008	0.04	0.03
			6	0.008	0.007	0.006	0.006	0.03	0.01
			9	0.007	0.006	0.006	0.006	0.03	0.01
).9	0.9	20	3	0.038	0.036	0.030	0.030	0.14	0.09
			6	0.036	0.034	0.028	0.028	0.13	0.04
			9	0.036	0.034	0.028	0.028	0.13	0.03
		60	3	0.012	0.010	0.009	0.009	0.05	0.03
			6	0.011	0.010	0.009	0.009	0.04	0.02
			9	0.011	0.010	0.008	0.009	0.04	0.01
		100	3	0.007	0.006	0.005	0.005	0.03	0.02
			6	0.007	0.006	0.005	0.005	0.03	0.01
			9	0.007	0.005	0.005	0.005	0.03	0.01

Table	1.11	Empiric	al $(\hat{\sigma}_{\rho}^{2})$) vari	ances	of ML	and	REML (estimat	ors of	ξ _{ρ_g a}	nd
means	of ja	ckknife	$(\hat{\sigma}_{J}^{2})$ a	nd boo	tstrap	$(\hat{\sigma}_{B}^{2})$	var	iances	of ML	estim	ators	of
$\rho_{\rm g}.$												

								ML	
				$\hat{\sigma}_{\mu}$	$\hat{\sigma}_{\rho}^{2}$		$\hat{\sigma}_{\rm B}^{\ 2}$		
H _a	H _b	n	r	REML	ML	$\hat{\sigma}_{\rm J}{}^2$	b = 100	Ъ – 500	
0.1	0.1	20	3	0.324	0.315	1.974	0.219	0.219	
			6	0.242	0.257	1.261	0.232	0.232	
			9	0.187	0.192	0.719	0.204	0.203	
		60	3	0.246	0.251	2.655	0.205	0.205	
			6	0.109	0.109	0.409	0.129	0.129	
			9	0.059	0.059	0.102	0.072	0.072	
		100	3	0.188	0.189	2.230	0.176	0.176	
			6	0.057	0.057	0.137	0.072	0.071	
			9	0.030	0.030	0.036	0.034	0.034	
0.1	0.5	20	3	0.291	0.234	1.299	0.199	0.198	
			6	0.173	0.159	0.753	0.170	0.171	
			9	0.111	0.110	0.394	0.137	0.137	
		60	3	0.155	0.124	1.526	0.125	0.126	
			6	0.045	0.043	0.220	0.065	0.066	
			9	0.026	0.026	0.051	0.035	0.035	
		100	3	0.092	0.075	1.131	0.093	0.093	
			6	0.022	0.021	0.069	0.032	0.032	
			9	0.014	0.014	0.016	0.017	0.017	
0.1	0.9	20	3	0.243	0.180	0.838	0.150	0.150	
			6	0.145	0.133	0.515	0.136	0.136	
			9	0.101	0.096	0.300	0.114	0.114	
		60	3	0.118	0.099	0.967	0.104	0.104	
			6	0.039	0.039	0.160	0.054	0.054	
			9	0.025	0.024	0.035	0.031	0.031	
		100	3	0.067	0.061	0.849	0.075	0.075	
			6	0.020	0.020	0.036	0.028	0.028	
			9	0.014	0.014	0.015	0.015	0.015	

							ML	
				$\hat{\sigma}_{\mu}$	$\hat{\sigma}_{\rho}^{2}$		$\hat{\sigma}_{\rm B}^{\ 2}$	
H _a	H _b	n	r	REML	ML	$\hat{\sigma}_{J}^{2}$	b = 100	b = 500
0.5	0.5	20	3	0.071	0.069	0.112	0.081	0.081
			6	0.044	0.044	0.052	0.047	0.001
			9	0.038	0.038	0.044	0.039	0.039
		60	3	0.018	0.018	0.020	0.019	0.019
			6	0.012	0.012	0.013	0.013	0.013
			9	0.011	0.011	0.012	0.011	0.011
		100	3	0.010	0.010	0.011	0.011	0.011
			6	0.007	0.007	0.007	0.007	0.007
			9	0.006	0.006	0.007	0.006	0.006
	0.9	20	3	0.047	0.046	0.065	0.054	0.054
			6	0.035	0.035	0.042	0.036	0.036
			9	0.033	0.033	0.038	0.033	0.033
		60	3	0.013	0.013	0.014	0.013	0.013
			6	0.011	0.011	0.011	0.011	0.011
			9	0.010	0.010	0.010	0.010	0.010
		100	3	0.007	0.007	0.008	0.007	0.007
			6	0.006	0.006	0.006	0.006	0.006
			9	0.006	0.006	0.006	0.006	0.006
).9	0.9	20	3	0.031	0.031	0.036	0.030	0.030
			6	0.030	0.030	0.034	0.028	0.028
			9	0.029	0.029	0.033	0.028	0.028
		60	3	0.009	0.010	0.010	0.009	0.009
			6	0.009	0.009	0.009	0.009	0.009
			9	0.009	0.009	0.009	0.008	0.008
		100	3	0.005	0.006	0.006	0.005	0.005
			6	0.005	0.005	0.005	0.005	0.005
			9	0.005	0.005	0.005	0.005	0.005

References

- Amemiya, Y (1985). What should be done when an estimated between-group covariance matrix is not nonnegative definite? The American Statistician 39:112-117.
- Baker, R. J. (1986). Selection indices in plant breeding. CRC Press, Inc. Boca Raton, Florida.
- Efron, B (1982). The Jackknife, the Bootstrap and other resampling plans. Philadelphia:SIAM.
- Falconer, D. S. (1981). Introduction to quantitative genetics. Edition 2. Longman, London.
- Hill, W. G. and R. Thompson (1978). Probabilities of nonpositive definite between-group or genetic covariance matrices. Biometrics 34:429-439.
- Harville, D. A. (1977). Maximum likelihood approaches to variance component estimation and to related problems. Journal of the American Statistical Association. 72:320-338.
- Johnson, M. E. (1987). Multivariate statistical simulation. John Wiley & Son, New York.
- Kinderman, A. L. (1975). Computer generation of random variables with normal and Studnet's T distributions. In: Proceedings of the statistical computing section, The American Statistical Association.

- Klotz, J. and J. Putter (1969). Maximum likelihood estimation of multivariate covariance components for the balanced one-way layout. The Annals of Mathematical Statistics 40:1100-1105.
- Knapp, S. J., W. C. Bridges, Jr. and M. H. Yang (1989). Nonparametric confidence interval estimators for heritability and expected selection response. Genetics 121:891-898.
- Lande, R. (1984). The genetic correlation between characters maintained by selection, linkage and inbreeding. Genetic Research 44:309-320.
- Miller, R. G. (1974). The jackknife-a review. Biometrika 61:115.
- Rao, C. R. and J. Kleffe (1988). Estimation of variance components and applications. North-Holland, Amsterdam.
- Scheinberg, E (1966). The sampling variance of the correlation coefficients estimated in genetic experiments. Biometrics 22:187-191.
- Searle, S. R. (1970) Linear Models. John Wiley & Sons, New York.
- Swallow, W. H. and J. F. Monahan (1984). Monte Carlo comparison of ANOVA, MIVQUE, REML, and ML estimators of variance components. Technometrics 26:47-57.
- VanVleck, L. D. and C. R. Henderson (1961). Empirical sampling estimates of genetic correlations. Biometrics 17:359-371.

CHAPTER 3

CONFIDENCE INTERVAL ESTIMATORS FOR MANOVA AND ML ESTIMATORS OF GENETIC CORRELATION

Abstract

Parametric interval estimators have been difficult to derive for many quantitative genetic parameters because their distributions are unknown. This has certainly been true for genetic correlation (ρ_g). Approximate estimators of the variance of multivariate analysis of variance (MANOVA) estimator of ρ_{g} have been described, but they are not valid in many situations. In addition, methods for estimating intervals of MANOVA and maximum likelihood (ML) estimator of ρ_{g} have not developped yet. Our objective was to evaluate the validity of normal-approximation parametric, jackknife, and bootstrap intervals and percentile and biascorrected percentile bootstrap intervals of MANOVA and ML estimators of ρ_{g} using computer simulation. Simulations were done using a balanced one-way linear model with two correlated traits. Estimated coverage probabilities (ECP) of parametric intervals were consistently significantly different from stated coverage probabilities (SCP). The parametric intervals were often wide and had negative lower bounds. ECPs for normal-approximation jackknife and bootstrap intervals were significantly different from SCPs. ECPs for MANOVA and ML percentile bootstrap intervals were relatively close to SCPs. ECPs of MANOVA and ML biascorrected bootstrap intervals were close to SCPs and the intervals were comparatively narrow. Intervals of MANOVA estimators were consistently wider than those of ML

estimators. The ML bias-corrected bootstrap percentile interval gave valid coverage and had narrow average interval length. We found number of genotypes used was more important for reducing interval lengths than the number of replications.

Key words: bootstrapping, jackknifing, maximum likelihood, MANOVA, genetic correlation.

Introduction

Parametric interval estimators have been difficult to find for many genetic parameters because their distributions are unknown. This has been shown for expected selection response (Knapp et al. 1989; Bridges et al. 1990) and is a problem for genetic correlation (ρ_g) as well. The distribution of ρ_g is unknown; however, we empirically estimated the distribution of multivariate analysis of variance (MANOVA), maximum likelihood (ML), and restricted maximum likelihood (REML) estimates of $\hat{\rho}_{g}$ in Chapter 2. MANOVA estimates were found to be approximately normally distributed regardless of the value of ρ_{g} , whereas ML and REML estimates of ρ_{g} were found to be approximately normally distributed or negatively or positively skewed (Liu and Knapp 1991). The shape of the distribution of ML or REML estimates is a function of the sign and magnitude of $\rho_{\rm g}.$ The distribution is negatively skewed when ρ_{g} is positive and approaches 1.0, positively skewed when ρ_g is negative and approaches -1.0, and approximately normally distribution when ρ_g approaches 0.0. To make statistical inferences about estimates of genetic correlation, methods are needed to empirically estimate the distribution and variance of this parameter.

Parametric estimators of the variance of genetic correlation have been described (Falconer 1981; Reeve 1955; Robertson 1959; Scheinberg 1966; Tallis 1959) but these estimators have not been widely used, perhaps because they are complex and their validity has been uncertain. We have shown the estimators described by Scheinberg (1966) and Falconer (1981) are not valid in many situations. Furthermore, these estimators strictly apply to MANOVA estimators of ρ_g . Other methods of estimating sampling variance are needed for ML and REML estimators of ρ_g .

Fast, efficient, and inexpensive computing technology has made it practical and feasible to apply data resampling methods, especially bootstrapping, to a wide range of statistical inference problems arising in population and quantitative genetics. Bootstrapping has been used, for example, to estimate variances of mating system parameters (Schoen and Clegg 1988), cumulative density functions (CDFs) and bias-corrected percentile (BCP) intervals of outcrossing rates (Knapp et al. 1991), and BCP intervals of ρ_g (Riska et al. 1989). Delete-one jackknifing has been used to estimate intervals for heritability and other genetic parameters (Knapp et al. 1989; Mitchell-Olds and Bergelson 1990).

Jackknifing and bootstrapping are tremendously versatile statistical tools because they can be applied to estimation problems where the distribution of the parameters are unknown or the validity of parametric methods are inadequate or sensitive to distributional or model assumptions (Miller 1974; Efron 1982), e.g., the estimation of intervals for variances (Miller 1974) and family-mean heritability

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(Arvesen and Schmitz 1970; Knapp et al. 1989). Their strength is magnified by their simplicity -- these methods are applied the same regardless of the parameter being estimated. It is this versatility and power which led us to investigate the validity of these methods for estimating confidence intervals of genetic correlation coefficients. Furthermore, there are no known parametric methods for estimating variances and intervals of ML and REML estimators of genetic correlation; however, we have shown bootstrapping can be used to get valid estimates of the variance of REML or ML estimators of ρ_{g} . In this paper, we report a simulation study carried out to estimate the validity of estimators of normal-approximation parametric, jackknife, and bootstrap and percentile and bias-corrected percentile bootstrap intervals of MANOVA, ML, and REML estimators of PR.

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Materials and Methods

The statistical model, simulation methods, and parameter values we used have been described (Chapter 2). MANOVA, ML, and REML methods were used to estimate $\hat{\rho}_s$; however, we do not report REML estimators because the interval coverage were, for practical purposes, equivalent to those of ML estimators. In addition, data for n = 20 (number of genotypes) and n = 60 are not reported for interval estimation methods other than the bias-corrected percentile bootstrap method because their coverage were unsatisfactory. The validity or lack of validity of these intervals is shown by estimates for n = 100, so there is no need to report estimates for sample sizes less than 100. This is justified because the coverage of these intervals deteriorates as n decreases.

Two-sided confidence intervals were estimated using confidence coefficients of 0.80 and 0.95. Realized coverage probabilities were estimated (ECP) by counting the number of interval estimates which covered the parameter value and dividing by the total number of estimates. Standard errors were estimated and used to test whether or not an estimate was significantly different from the stated coverage probability (SCP) using a Type I error probability of 0.05.

Normal-approximation (NA) intervals: Normalapproximation intervals were estimated using Scheinberg (1966) $(\hat{\sigma}_s^2)$ (NAS), Falconer (1981) $(\hat{\sigma}_F^2)$ (NAF), jackknife $(\hat{\sigma}_{g}^{2})$ (NAJ), and bootstrap $(\hat{\sigma}_{B}^{2})$ (NAB) variances of ρ_{g} . A (1 - α)100% two-sided normal-approximation interval of ρ_{g} using the parametric variances is

$$\{\hat{\rho}_{g} - Z_{1-\alpha}(\hat{\sigma}_{P}^{2})^{\frac{1}{4}}, \hat{\rho}_{g} + Z_{1-\alpha}(\hat{\sigma}_{P}^{2})^{\frac{1}{4}}\}$$
 (1)

where $\hat{\rho}_{g}$ is the MANOVA estimate of ρ_{g} , $Z_{1-\alpha}$ is the $(1 - \alpha)100$ % two-sided critical value of the standard normal distribution, and $\hat{\sigma}_{p}^{2}$ is estimated parametric variance of $\hat{\rho}_{g}$, either $\hat{\sigma}_{s}^{2}$ or $\hat{\sigma}_{F}^{2}$. The square root of $\hat{\sigma}_{F}^{2}$ is negative when $\hat{\rho}_{g} > 1.0$ or < -1.0 and the interval does not cover ρ_{g} .

A $(1 - \alpha)100$ % two-sided normal-approximation interval of ρ_g using the nonparametric variance is (Efron 1982)

$$\{\hat{\rho}_{g} - t_{1-\alpha:s-1}(\hat{\sigma}_{N}^{2})^{\frac{1}{4}}, \hat{\rho}_{g} + t_{1-\alpha:s-1}(\hat{\sigma}_{N}^{2})^{\frac{1}{4}}\}$$
(2)

where $t_{1-\alpha;s-1}$ is $(1-\alpha)100$ % two-sided critical value of the t-distribution with s - 1 degrees of freedom, s is the number of samples used for a particular resampling method, and $\hat{\sigma}_{N}^{2} = \hat{\sigma}_{J}^{2}$ or $\hat{\sigma}_{B}^{2}$.

Bootstrap percentile (BP) and bias-corrected percentile (BCP) intervals: Given the cumulative distribution function (CDF) of the bootstrap point estimate (Efron 1982)

 $\hat{CDF}(x) = Prob \{ \hat{\rho}_g \leq x \},\$

then (1 - α)100% interval of ρ_g is

 $\{C\hat{D}F^{-1}(\alpha), C\hat{D}F^{-1}(1-\alpha)\}.$ (3)

A (1 - α)100% bias-corrected percentile interval for ρ_g is (Efron 1982)

$$\{C\hat{D}F^{-1}[\Phi(2z_0 - z_{\alpha})], C\hat{D}F^{-1}[(\Phi(2z_0 + z_{\alpha})]\}$$
(4)

where $z_0 = \Phi^{-1}[CDF(\hat{\rho}_g)]$, $z_{\alpha} = \Phi^{-1}(1 - \alpha)$, and Φ is the CDF for a standard normal variate.

Results

Normal-approximation intervals: The estimated coverage probabilities (ECP) for the NAS intervals were significantly greater than the state coverage probabilities (SCP) (Table 2.1). ECPs of the NAF intervals were usually less than the SCPs when H_a and H_b were less than 0.5 and $\rho_g = 0.5$ or 0.9 (Table 2.2). The ECPs were usually greater than the SCPs when H_a and H_b were greater than or equal to 0.5, r = 3 or 6, and $\rho_g = 0.1$ or 0.5, but were significantly less than the SCPs when r = 9 (Table 2.2). The intervals of NAS were consistently very wide when H_a and H_b were less than 0.5 (Table 2.3). The interval lengths of NAF were meaningless when H_a or H_b was less than 0.5 because a proportion of the point estimates were < -1.0 or > 1.0 (Chapter 2), which leads to negative interval lengths. Interval lengths decreased as n and r increased. The effect of n was greater than the effect of r (Table 2.3).

[Table 2.1, 2.2, and 2.3 placement]

ECPs for the NAJ intervals of MANOVA and ML estimators were significantly less than the SCPs (Table 2.4 and 2.5). The intervals were wide when H_a or H_b was less than or equal to 0.5 (Table 2.6).

[Table 2.4, 2.5, and 2.6 placement]

ECPs for the NAB intervals of MANOVA and ML estimators were significantly less than the SCPs (Table 2.7 and 2.8). Interval lengths were decreased as $\rho_{\rm g}$, r, H_a, and H_b increased, but the effect of r decreased as $\rm H_{a}$ and $\rm H_{b}$ increased.

[Table 2.7, 2.8, and 2.9 placement]

Percentile (BP) and bias-corrected percentile bootstrap intervals (BCP): ECPs for BP intervals closely approached the SCPs as n and r increased (Table 2.10). ECPs for ML estimates were closer to the SCPs than those of MANOVA estimates (Table 2.10 and 2.11). Intervals of the MANOVA estimates were wider than those of the ML estimates when either H_a or H_b was 0.5 or lower (Table 2.12). Intervals of MANOVA and ML estimators were more narrow and the difference between them were small when both H_a and H_b were 0.5 or higher (Table 2.12). The interval length could be reduced by increasing n and r, but the effect of increasing r was diminished when both H_a and H_b was 0.9.

[Table 2.10, 2.11, and 2.12 placement]

ECPs of MANOVA BCP intervals were consistently less than the SCPs when H_a and H_b were less than 0.5 (Table 2.13). When H_a and H_b were 0.5 or higher the ECPs were closer to the SCPs. ECPs of ML BCP intervals were close to the SCPs (Table 2.14). Interval lengths of MANOVA BCP intervals were wider than these of ML BCP intervals when H_a and H_b were 0.5 or less (Table 2.15). Interval length could be decreased by increasing n and r, but the effect of r diminished as heritabilities increased.

[Table 2.13, 2.14, and 2.15 placement]

Discussion

The parametric normal-approximation intervals of ρ_g gave extremely unsatisfactory coverage (Tables 1 & 2). These estimators fail because the Scheinberg (1966) and Falconer (1981) variances do not give valid estimates of the variance of MANOVA estimates of ρ_g (Chapter 2).

Bootstrapping and jackknifing are effective tools for estimating the variances and biases of many complex parameter estimates; however, they are more prone to fail as tools for estimating intervals than as tools for estimating variances and biases (Efron 1987; Schenker 1985). This is particularly true of parameters which do not have symmetric distributions or distributions whose shapes change as the parameter value changes. ML estimators of ρ_g fit this definition. We have shown the shape of the distribution of ML estimates of ρ_g is a function of the sign and magnitude of ρ_g (Chapter 2). This is problematic because the tails of bootstrap distributions are used to define confidence regions (Efron 1987; Schenker 1985).

Nevertheless, we have shown the ML BCP intervals of ρ_g give valid coverage when the heritabilities are greater than or equal to 0.5 (Table 2.14). Their coverage breaks down if the heritability of either trait is equal to 0.1. We know the variance of ρ_g increases as heritability decreases, but this alone does not explain why the ML BCP interval of ρ_g deteriorates as heritability decreases below a certain

65

value. After all, we have shown bootstrapping is an effective way of getting valid estimates of the variance of MANOVA or ML estimator of ρ_g (Chapter 2). The coverage was slightly unsatisfactory when $\rho_g = 0.9$.

The other methods, whether they were applied to MANOVA or ML estimator of $\rho_{\rm g}$, were less satisfactory than the bias-corrected percentile method applied to ML estimator of $\rho_{\rm g}$, although the BCP intervals of MANOVA estimator of $\rho_{\rm g}$ were a close second. None of the normal-approximation methods worked and jackknifing failed altogether. There is no rationale for using the percentile method to estimate intervals because the bias-corrected percentile method is, either theoretically or empirically, always superior to the percentile method. They either give equivalent coverage or the BCP method gives superior coverage, whether applied to $\rho_{\rm g}$ or any other parameter.

The variances and interval lengths of MANOVA or ML estimator of ρ_8 are decreased by increasing n or r; however, greater efficiency is achieved by increasing n at the expense of r. This is consistent with experiment designs which have been found to maximize parameter estimation efficiency for variances or ratios of variances (Anderson and Crump 1967; McCutchan, Ou, and Namkoong 1985; Thompson 1975). Designs which use intentional unbalance may be optimum (Thompson 1975); however, these designs are variants of the completely randomized experiment design and may require unrealistically great numbers of homogeneous experimental units. These designs strive to maximize n by using a minimum number of replicated genotypes.

Percentile and bias-corrected percentile intervals have been widely used because they are simple and often effective tools for estimating intervals for parameters which have complex distributions. But theoretical criticisms of these methods have surfaced which show when and why they sometimes fail (Efron 1987; Efron and Tibshirani 1986; Schenker 1985). The main problems have been thoroughly outlined by Efron (1987), Efron and Tibshirani (1986), and Schenker (1985). The double bootstrap has been proposed to overcome these problems (Schenker 1985). The double bootstrap, if applied without using a sampling scheme designed to reduce the number of computations, uses b^2 bootstrap samples. If b =1000 bootstrap samples are drawn, then $b^* = 1000$ bootstrap samples would be drawn from each of these. This gives 1,000,000 bootstrap samples! This solution has obvious limitations. Stratified sampling schemes have been proposed to alleviate the computational difficulties imposed by the double bootstrap. We have not investigated the double bootstrap interval; however, it should give coverages closer to stated coverages than the BCP interval. The double bootstrap should be an effective way to estimate the biases of estimators of ρ_{g} . The jackknife and bootstrap failed to do this. If the double bootstrap succeeds where these

methods failed, then MANOVA and ML estimators of $\rho_{\rm g}$ can be bias corrected.

Our simulations strongly support using ML estimators of ρ_8 and BCP intervals. The greatest practical problem facing investigators is the lack of algorithms and software for these purposes. The algorithms we used for REML and ML estimation of variance-covariance matrix (Amemiya 1985; Klotz and Putter 1969) are limited to the one-factor linear model. The practical value of the our findings would be greatly increased by efficient and widely applicable computing solutions.

Table 2.1. Estimated coverage probabilities (ECP) of the normal-approximation interval of ρ_g estimated using the parametric variance estimator of Scheinberg (1966) $(\hat{\sigma}_s^2)$. MANOVA was used to estimate ρ_g and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r				
				3	6			9	
				Stated	coverage	probab	ilities		
Ha	H _b	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95	
0.1	0.1	0.1 0.5 0.9	0.98* 0.99* 1.00*	1.00* 1.00* 1.00*	0.99* 0.98* 1.00*	1.00* 1.00* 1.00*	0.99* 0.98* 0.99*	1.00* 1.00* 1.00*	
	0.5	0.1 0.5 0.9	0.99* 0.99* 0.99*	1.00* 1.00* 1.00*	0.98* 0.99* 1.00*	1.00* 1.00* 1.00*	0.98* 0.98* 1.00*	1.00* 1.00* 1.00*	
	0.9	0.1 0.5 0.9	0.99* 1.00* 0.99*	1.00* 1.00* 1.00*	0.98* 0.99* 1.00*	1.00* 1.00* 1.00*	0.98* 0.99* 0.99*	1.00* 1.00* 1.00*	
0.5	0.5	0.1 0.5 0.9	0.98* 0.98* 0.98*	1.00* 1.00* 1.00*	0.99* 0.98* 0.98*	1.00* 1.00* 1.00*	0.99* 0.98* 0.97*	1.00* 1.00* 1.00*	
	0.9	0.1 0.5 0.9	0.98* 0.98* 0.99*	1.00* 1.00* 1.00*	0.99* 0.98* 0.98*	1.00* 1.00* 1.00*	0.99* 0.98* 0.97*	1.00* 1.00* 1.00*	
0.9	0.9	0.1 0.5 0.9	0.98* 0.98* 0.97*	1.00* 1.00* 1.00*	0.99* 0.98* 0.97*	1.00* 1.00* 1.00*	0.98* 0.99* 0.98*	1.00* 1.00* 1.00*	

Table 2.2. Estimated coverage probabilities (ECP) of the normal-approximation interval of ρ_g estimated using the parametric variance estimator of Falconer (1981) $(\hat{\sigma}_F^2)$. MANOVA was used to estimate ρ_g and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r			
			:	3			9	
				Stated	coverage	probab	ilities	
Ha	H _b	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95
0.1	0.1	0.1 0.5 0.9	0.69* 0.64* 0.44*	0.78* 0.71* 0.49*	0.84* 0.80 0.49*	0.93 0.88* 0.56*	0.90* 0.85* 0.55*	0.97* 0.93* 0.64*
	0.5	0.1 0.5 0.9	0.85* 0.77* 0.45*	0.93 0.85* 0.56*	0.89* 0.83* 0.50*	0.96* 0.92* 0.64*	0.88* 0.85* 0.50*	0.97* 0.94 0.65*
	0.9	0.1 0.5 0.9	0.87* 0.75* 0.37*	0.95 0.82* 0.57*	0.86* 0.80 0.39*	0.95 0.90* 0.57*	0.85* 0.81 0.43*	0.96* 0.93* 0.61*
0.5	0.5	0.1 0.5 0.9	0.95* 0.93* 0.71*	0.99* 0.98* 0.79*	0.91* 0.90* 0.75*	0.98* 0.98* 0.87*	0.86* 0.85* 0.73*	0.98* 0.96* 0.87*
	0.9	0.1 0.5 0.9	0.95* 0.93* 0.76*	0.99* 0.98* 0.86*	0.89* 0.87* 0.75*	0.98* 0.97* 0.89*	0.83* 0.81 0.72*	0.96 0.95 0.88*
0.9	0.9	0.1 0.5 0.9	0.95* 0.95* 0.89*	0.99* 0.99* 0.97*	0.86* 0.85* 0.83*	0.97* 0.96* 0.94	0.77 0.76* 0.73*	0.93* 0.92* 0.92*

Table 2.3. Estimated lengths of normal-approximation intervals of $\rho_{\rm g}$ estimated using the parametric variance estimators of Scheinberg (1966) ($\hat{\sigma}_{\rm S}^2$) and Falconer (1981) ($\hat{\sigma}_{\rm F}^2$) estimated using MANOVA (n = 100, 1 - α = 0.95).

				r						
				$\hat{\sigma}_{s}^{2}$			$\hat{\sigma}_{\rm F}^{\ 2}$			
Ha	H_{b}	ρ _g	3	6	9	3	6	9		
0.1	0.1	0.1	24.55	2.51	1.65	-4.12	1.33	1.13		
		0.5	229.86	2.00	1.37	-49.51	1.02	0.86		
		0.9	20.41	66.23	1.00	0.45	-10.30	0.22		
	0.5	0.1	7.25	1.43	1.18	1.26	0.94	0.76		
		0.5	4.25	1.92	0.98	0.91	0.69	0.58		
		0.9	10.57	1.17	0.67	0.27	0.17	0.13		
	0.9	0.1	5.48	1.32	1.11	1.11	0.81	0.66		
		0.5	13.35	1.26	0.95	0.76	0.59	0.49		
		0.9	247.76	2.54	0.67	0.24	0.14	0.11		
0.5	0.5	0.1	1.05	0.91	0.86	0.88	0.63	0.51		
		0.5	0.83	0.70	0.66	0.67	0.47	0.39		
		0.9	0.43	0.27	0.22	0.16	0.12	0.10		
	0.9	0.1	0.91	0.84	0.82	0.76	0.54	0.44		
		0.5	0.73	0.66	0.63	0.58	0.41	0.33		
		0.9	0.31	0.22	0.19	0.14	0.10	0.08		
0.9	0.9	0.1	0.80	0.79	0.78	0.66	0.46	0.38		
		0.5	0.61	0.60	0.59	0.50	0.35	0.29		
		0.9	0.18	0.17	0.16	0.13	0.09	0.07		

r

Table 2.4. Estimated coverage probabilities (ECP) of the normal-approximation jackknife interval of ρ_8 estimated using MANOVA and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r			
				3	6			9
				Stated	coverage	probab	ilities	
Ha	H _b	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95
0.1	0.1	0.1 0.5 0.9	0.31* 0.32* 0.33*	0.52* 0.51* 0.52*	0.35* 0.44* 0.48*	0.52* 0.59* 0.63*	0.41* 0.54* 0.56*	0.57* 0.70* 0.74*
	0.5	0.1 0.5 0.9	0.35* 0.30* 0.35*	0.63* 0.58* 0.59*	0.41* 0.48* 0.54*	0.62* 0.67* 0.73*	0.48* 0.58* 0.61*	0.67* 0.76* 0.84*
	0.9	0.1 0.5 0.9	0.31* 0.28* 0.34*	0.65* 0.56* 0.57*	0.38* 0.46* 0.54*	0.62* 0.65* 0.71*	0.47* 0.56* 0.61*	0.65* 0.75* 0.83*
0.5	0.5	0.1 0.5 0.9	0.57* 0.63* 0.61*	0.74* 0.87* 0.89*	0.64* 0.62* 0.60*	0.86* 0.89* 0.88*	0.62* 0.60* 0.60*	0.86* 0.87* 0.88*
	0.9	0.1 0.5 0.9	0.61* 0.62* 0.59*	0.83* 0.90* 0.90*	0.62* 0.60* 0.61*	0.85* 0.88* 0.89*	0.60* 0.60* 0.59*	0.85* 0.88* 0.88*
0.9	0.9	0.1 0.5 0.9	0.60* 0.61* 0.61*	0.85* 0.88* 0.89*	0.61* 0.59* 0.59*	0.85* 0.87* 0.89*	0.62* 0.61* 0.60*	0.86* 0.88* 0.89*

Table 2.5. Estimated coverage probabilities (ECP) of the normal-approximation jackknife interval of ρ_g estimated using ML and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r			
			:	3	6		9	
				Stated	coverage	probab	ilities	
Ha	H _b	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95
0.1	0.1	0.1 0.5 0.9	0.24* 0.26* 0.29*	0.46* 0.48* 0.50*	0.26* 0.35* 0.41*	0.50* 0.54* 0.57*	0.31* 0.44* 0.49*	0.53* 0.63* 0.68*
	0.5	0.1 0.5 0.9	0.30* 0.27* 0.30*	0.62* 0.57* 0.56*	0.33* 0.40* 0.47*	0.60* 0.62* 0.68*	0.37* 0.50* 0.56*	0.61* 0.69* 0.79*
	0.9	0.1 0.5 0.9	0.26* 0.26* 0.30*	0.61* 0.56* 0.55*	0.30* 0.38* 0.46*	0.60* 0.59* 0.66*	0.36* 0.48* 0.56*	0.60* 0.68* 0.78*
0.5	0.5	0.1 0.5 0.9	0.47* 0.60* 0.61*	0.65* 0.83* 0.87*	0.59* 0.61* 0.60*	0.79* 0.88* 0.88*	0.61* 0.60* 0.60*	0.83* 0.87* 0.88*
	0.9	0.1 0.5 0.9	0.54* 0.61* 0.59*	0.74* 0.89* 0.89*	0.60* 0.60* 0.61*	0.82* 0.88* 0.89*	0.60* 0.60* 0.59*	0.84* 0.88* 0.88*
0.9	0.9	0.1 0.5 0.9	0.60* 0.61* 0.61*	0.85* 0.88* 0.89*	0.61* 0.59* 0.59*	0.85* 0.87* 0.89*	0.62* 0.61* 0.60*	0.86* 0.88* 0.89*

Table 2.6. Estimated lengths of the normal-approximation jackknife interval of ρ_8 estimated using MANOVA and ML (n = 100, and 1 - α = 0.95).

					:	r			
				MANOVA			ML		
Ha	H_{b}	ρ _g	3	6	9	3	6	9	
0.1	0.1	0.1 0.5 0.9	6.38 5.76 7.93	1.15 1.06 1.00	0.74 0.62 0.48	3.85 3.42 2.43	2.64 0.87 0.45	1.71 0.44 0.31	
	0.5	0.1 0.5 0.9	1.73 3.36 6.97	0.63 0.60 0.64	0.51 0.43 0.29	3.20 2.43 1.57	1.94 0.59 0.35	1.16 0.31 0.23	
	0.9	0.1 0.5 0.9	1.75 3.06 4.86	0.60 0.56 0.63	0.49 0.42 0.30	2.67 2.04 1.41	1.68 0.56 0.31	1.03 0.29 0.23	
0.5	0.5	0.1 0.5 0.9	0.45 0.36 0.18	0.38 0.30 0.11	0.37 0.28 0.09	0.44 0.22 0.17	0.29 0.15 0.11	0.25 0.12 0.09	
	0.9	0.1 0.5 0.9	0.39 0.31 0.13	0.36 0.28 0.09	0.35 0.27 0.08	0.34 0.17 0.13	0.24 0.12 0.09	0.22 0.11 0.08	
0.9	0.9	0.1 0.5 0.9	0.34 0.26 0.07	0.33 0.26 0.07	0.33 0.25 0.06	0.20 0.10 0.07	0.18 0.09 0.07	0.18 0.09 0.06	

Table 2.7. Estimated coverage probabilities (ECP) of the normal-approximation bootstrap (b = 500) interval of ρ_g estimated using MANOVA and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

				r							
			3		6		9				
				Stated	coverage	probab	ilities				
Ha	H_{b}	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95			
0.1	0.1	0.1 0.5 0.9	0.71* 0.73* 0.77	0.94 0.96 0.98*	0.65* 0.65* 0.69*	0.93* 0.92* 0.96	0.72* 0.61* 0.61*	0.94 0.88* 0.90*			
	0.5	0.1 0.5 0.9	0.67* 0.69* 0.78	0.94 0.94 0.96	0.62* 0.64* 0.71*	0.90* 0.91* 0.95	0.59* 0.59* 0.61*	0.88* 0.89* 0.90*			
	0.9	0.1 0.5 0.9	0.67* 0.72* 0.78	0.94 0.95 0.95	0.62* 0.65* 0.69*	0.89* 0.92* 0.96	0.59* 0.60* 0.62*	0.88* 0.89* 0.91*			
0.5	0.5	0.1 0.5 0.9	0.58* 0.58* 0.54*	0.88* 0.87* 0.83*	0.60* 0.58* 0.56*	0.88* 0.87* 0.86*	0.59* 0.60* 0.58*	0.88* 0.88* 0.87*			
	0.9	0.1 0.5 0.9	0.55* 0.59* 0.58*	0.87* 0.87* 0.85*	0.58* 0.58* 0.57*	0.88* 0.87* 0.86*	0.60* 0.58* 0.57*	0.89* 0.88* 0.87*			
0.9	0.9	0.1 0.5 0.9	0.57* 0.56* 0.59*	0.88* 0.87* 0.87*	0.58* 0.58* 0.61*	0.88* 0.87* 0.88*	0.58* 0.56* 0.57*	0.87* 0.88* 0.88*			

Table 2.8. Estimated coverage probabilities (ECP) of the normal-approximation bootstrap (b = 500) interval of ρ_g estimated using ML and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r			
			3		6		9	
				Stated	coverage	probab	ilities	
Ha	H _b	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95
0.1	0.1	0.1 0.5 0.9	0.67* 0.64* 0.63*	0.91* 0.92* 0.91*	0.60* 0.62* 0.71*	0.89* 0.89* 0.90*	0.59* 0.59* 0.60*	0.89* 0.87* 0.83*
	0.5	0.1 0.5 0.9	0.67* 0.67* 0.73*	0.92* 0.93* 0.93*	0.61* 0.62* 0.69*	0.90* 0.89* 0.89*	0.59* 0.58* 0.59*	0.88* 0.88* 0.81*
	0.9	0.1 0.5 0.9	0.68* 0.71* 0.72*	0.93 0.93 0.91*	0.60* 0.62* 0.67*	0.88* 0.91* 0.87*	0.58* 0.60* 0.58*	0.88* 0.88* 0.82*
0.5	0.5	0.1 0.5 0.9	0.58* 0.58* 0.53*	0.88* 0.87* 0.81*	0.60* 0.58* 0.56*	0.88* 0.87* 0.86*	0.59* 0.60* 0.58*	0.88* 0.88* 0.87*
	0.9	0.1 0.5 0.9	0.55* 0.59* 0.58*	0.87* 0.87* 0.85*	0.58* 0.58* 0.57*	0.88* 0.87* 0.86*	0.60* 0.58* 0.57*	0.89* 0.88* 0.87*
0.9	0.9	0.1 0.5 0.9	0.57* 0.56* 0.59*	0.88* 0.87* 0.87*	0.58* 0.58* 0.61*	0.88* 0.87* 0.88*	0.58* 0.56* 0.57*	0.87* 0.88* 0.88*

Table 2.9. Estimated lengths of the normal-approximation bootstrap (b = 500) intervals of ρ_g estimated using MANOVA and ML (n = 100 and 1 - α = 0.95).

		•			r					
				MANOVA			ML			
H _a	H _b	ρ _g	3	6	9	3	6	9		
0.1	0.1	0.1 0.5 0.9	4.30 4.06 4.65	1.49 1.22 1.46	0.80 0.66 0.54	1.39 1.33 1.23	0.99 0.85 0.57	0.74 0.61 0.32		
	0.5	0.1 0.5 0.9	1.42 1.62 2.53	0.72 0.72 0.81	0.52 0.48 0.38	0.95 0.92 0.89	0.64 0.57 0.37	0.51 0.43 0.22		
	0.9	0.1 0.5 0.9	1.22 1.69 2.56	0.67 0.77 0.90	0.49 0.43 0.37	0.82 0.86 0.83	0.60 0.54 0.36	0.48 0.42 0.22		
0.5	0.5	0.1 0.5 0.9	0.44 0.35 0.16	0.37 0.29 0.11	0.35 0.28 0.09	0.44 0.35 0.15	0.37 0.29 0.11	0.35 0.28 0.09		
	0.9	0.1 0.5 0.9	0.38 0.30 0.12	0.35 0.27 0.09	0.34 0.26 0.08	0.38 0.30 0.12	0.35 0.27 0.09	0.34 0.26 0.08		
0.9	0.9	0.1 0.5 0.9	0.33 0.26 0.07	0.32 0.25 0.07	0.32 0.25 0.07	0.33 0.26 0.07	0.32 0.25 0.07	0.32 0.25 0.07		

Table 2.10. Estimated coverage probabilities (ECP) of the percentile bootstrap (b = 500) interval of ρ_g estimated using MANOVA and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r				
			:	3	6		9		
				Stated	coverage	probab	ilities		
H _a	H_{b}	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95	
0.1	0.1	0.1 0.5 0.9	0.72* 0.71* 0.67*	0.88* 0.88* 0.85*	0.76* 0.76* 0.73*	0.92* 0.92* 0.88*	0.78 0.77* 0.74*	0.94 0.93* 0.90*	
	0.5	0.1 0.5 0.9	0.75* 0.72* 0.72*	0.92* 0.90* 0.89*	0.77* 0.77* 0.77*	0.93* 0.92* 0.91*	0.77 0.77 0.73*	0.93* 0.93 0.90*	
	0.9	0.1 0.5 0.9	0.78 0.75* 0.72*	0.93* 0.91* 0.90*	0.77 0.77 0.73*	0.92* 0.92* 0.90*	0.79 0.78 0.75*	0.94 0.94 0.90*	
0.5	0.5	0.1 0.5 0.9	0.78 0.77 0.72*	0.93* 0.93* 0.90*	0.80 0.78 0.76*	0.94 0.93 0.93*	0.79 0.78 0.77*	0.93 0.94 0.93*	
	0.9	0.1 0.5 0.9	0.76* 0.78 0.76*	0.92* 0.92* 0.91*	0.78 0.77 0.76*	0.95 0.93* 0.92*	0.79 0.78 0.78	0.94 0.94 0.92*	
0.9	0.9	0.1 0.5 0.9	0.78 0.77* 0.77*	0.93 0.93* 0.92*	0.79 0.78 0.78	0.94 0.94 0.93	0.78 0.77 0.77*	0.93* 0.93* 0.94	

Table 2.11. Estimated coverage probabilities (ECP) of the percentile bootstrap (b = 500) interval of ρ_g estimated using and n = 100. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r				
				3	6		9		
				Stated	coverage	probab	ilities		
H _a	H _b	ρ _g	0.80	0.95	0.80	0.95	0.80	0.95	
0.1	0.1	0.1 0.5 0.9	0.79 0.83* 0.83*	0.95 0.96* 0.96*	0.77* 0.78 0.77	0.93* 0.94 0.93	0.78 0.77 0.74*	0.94 0.93* 0.91*	
	0.5	0.1 0.5 0.9	0.81 0.82* 0.85*	0.95 0.96 0.96*	0.78 0.78 0.79	0.94 0.94 0.95	0.77 0.77 0.73*	0.93* 0.93 0.91*	
	0.9	0.1 0.5 0.9	0.83* 0.85* 0.87*	0.96* 0.96* 0.97*	0.78 0.79 0.76*	0.93* 0.94 0.94	0.79 0.78 0.75*	0.94 0.94 0.90*	
0.5	0.5	0.1 0.5 0.9	0.78 0.77 0.72*	0.93* 0.93* 0.90*	0.80 0.78 0.76*	0.94 0.93 0.93*	0.79 0.78 0.77*	0.93 0.94 0.93*	
	0.9	0.1 0.5 0.9	0.76* 0.78 0.76*	0.92* 0.92* 0.91*	0.78 0.77 0.76*	0.95 0.93* 0.92*	0.79 0.78 0.78	0.94 0.94 0.92*	
0.9	0.9	0.1 0.5 0.9	0.78 0.77* 0.77*	0.93 0.93* 0.92*	0.79 0.78 0.78	0.94 0.94 0.93	0.78 0.77 0.77*	0.93* 0.93* 0.94	

Table 2.12.	Estimated lengths of the percentile bootstrap (k	С
= 500) inter	rvals of $ ho_{g}$ estimated using MANOVA and ML (n =	
100, and 1 -	$\alpha = 0.95).$	

			r							
			MANOVA			ML				
H _a	H _b	$ ho_{g}$	3	6	9	3	6	9		
0.1	0.1	0.1 0.5 0.9	14.13 8.19 5.18	3.54 2.63 2.59	1.13 0.87 0.90	1.49 1.52 1.52	1.20 1.10 0.98	0.91 0.77 0.51		
	0.5	0.1 0.5 0.9	2.67 2.50 2.60	1.12 1.10 1.53	0.63 0.59 0.68	1.16 1.14 1.24	0.80 0.71 0.65	0.62 0.53 0.34		
	0.9	0.1 0.5 0.9	2.08 2.52 2.23	0.92 1.20 1.63	0.59 0.58 0.65	1.00 1.00 1.06	0.74 0.67 0.62	0.59 0.51 0.33		
0.5	0.5	0.1 0.5 0.9	0.52 0.42 0.20	0.45 0.36 0.14	0.43 0.34 0.11	0.52 0.42 0.19	0.45 0.36 0.14	0.43 0.34 0.11		
	0.9	0.1 0.5 0.9	0.45 0.37 0.15	0.42 0.33 0.11	0.41 0.32 0.10	0.45 0.37 0.15	0.42 0.33 0.11	0.41 0.32 0.10		
0.9	0.9	0.1 0.5 0.9	0.40 0.31 0.09	0.39 0.30 0.08	0.39 0.30 0.08	0.40 0.31 0.09	0.39 0.30 0.08	0.39 0.30 0.08		

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Table 2.13. Estimated coverage probabilities (ECP) of the bias-corrected percentile bootstrap (b = 500) interval of ρ_g estimated using MANOVA. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

						r			
					3	6		9	
					Stated	coverag	e proba	 bilitie	:S
Ha	H_{b}	ρ _g	n	0.80	0.95	0.80	0.95	0.80	0.95
0.1	0.1	0.1	20	0.35*	0.50*	0.48*	0.65*	0.59*	0.76*
			60	0.48*	0.66*	0.64*	0.83*	0.72*	0.89*
			100	0.53*	0.74*	0.70*	0.87*	0.76*	0.93*
		0.5	20	0.33*	0.47*	0.43*	0.59*	0.53*	0.70*
			60	0.45*	0.63*	0.62*	0.80*	0.69*	0.87*
			100	0.50*	0.70*	0.69*	0.87*	0.75*	0.92*
		0.9	20	0.30*	0.43*	0.35*	0.49*	0.37*	0.53*
			60	0.40*	0.56*	0.49*	0.68*	0.59*	0.76*
			100	0.42*	0.59*	0.57*	0.77*	0.68*	0.85*
	0.5	0.1	20	0.52*	0.67*	0.61*	0.77*	0.65*	0.83*
			60	0.64*	0.81*	0.71*	0.88*	0.76*	0.91*
			100	0.66*	0.84*	0.75*	0.91*	0.77*	0.93*
		0.5	20	0.46*	0.60*	0.55*	0.72*	0.61*	0.77*
			60	0.57*	0.75*	0.65*	0.83*	0.73*	0.90*
			100	0.59*	0.77*	0.72*	0.89*	0.77*	0.93*
		0.9	20	0.39*	0.53*	0.40*	0.57*	0.44*	0.60*
			60	0.45*	0.62*	0.52*	0.71*	0.59*	0.78*
			100	0.47*	0.65*	0.62*	0.81*	0.67*	0.84*

					3		6		9	
					Stated	coverag	e proba	bilitie	25	
H _a	H _b	ρ _g	n	0.80	0.95	0.80	0.95	0.80	0.95	
	0.9	0.1	20	0.55*	0.69*	0.62*	0.78*	0.66*	0.81*	
			60	0.63*	0.81*	0.72*	0.89*	0.77	0.93*	
		0.5	100 20	0.68* 0.50*	0.86* 0.65*	0.74*	0.91*	0.79	0.94	
		0.5	20 60	0.50*	0.65*	0.56* 0.66*	0.71* 0.84*	0.62* 0.72*	0.77*	
			100	0.59*	0.74*	0.00*	0.84*	0.72*	0.88* 0.93*	
		0.9	20	0.45*	0.57*	0.71*	0.88*	0.43*	0.58*	
		0.5	60	0.45*	0.61*	0.52*	0.71*	0.43*	0.58*	
			100	0.48*	0.67*	0.57*	0.76*	0.68*	0.84*	
0.5	0.5	0.1	20	0.71*	0.88*	0.77*	0.91*	0.79	0.93*	
			60	0.79	0.94	0.78	0.93	0.79	0.94	
			100	0.79	0.94	0.80	0.94	0.80	0.94	
		0.5	20	0.72*	0.87*	0.77	0.93*	0.78	0.93	
			60	0.77	0.93*	0.77	0.93*	0.79	0.94	
			100	0.78	0.93	0.79	0.94	0.79	0.94	
		0.9	20	0.53*	0.69*	0.66*	0.82*	0.71*	0.87*	
			60	0.71*	0.89*	0.74*	0.91*	0.78	0.92*	
			100	0.72*	0.90*	0.76*	0.93	0.77	0.93*	
	0.9	0.1	20	0.77*	0.91*	0.79	0.94	0.79	0.93*	
			60	0.80	0.94	0.79	0.95	0.78	0.93*	
			100	0.77	0.93*	0.80	0.95	0.80	0.95	
		0.5	20	0.73*	0.89*	0.77*	0.92*	0.76*	0.91*	
			60	0.78	0.93	0.81	0.95	0.79	0.94	
			100	0.79	0.93*	0.78	0.94	0.79	0.94	
		0.9	20	0.56*	0.74*	0.68*	0.85*	0.73*	0.89*	
			60	0.72*	0.88*	0.75*	0.91*	0.77	0.94	
			100	0.75*	0.92*	0.77*	0.93*	0.78	0.93	

					r							
					3		6	9				
					Stated	coverag	e proba	bilitie	es			
Ha	H _b	ρ _g	n	0.80	0.95	0.80	0.95	0.80	0.95			
0.9	0.9	0.1 0.5 0.9	20 60 100 20 60 100 20 60 100	0.80 0.79 0.78 0.78 0.79 0.78 0.73* 0.76* 0.78	0.95 0.95 0.94 0.93 0.94 0.93 0.91* 0.92* 0.93*	0.79 0.79 0.80 0.79 0.80 0.78 0.73* 0.80 0.78	0.93 0.94 0.95 0.93 0.94 0.95 0.91* 0.94 0.94	0.80 0.79 0.79 0.78 0.78 0.78 0.75* 0.78 0.78	0.94 0.94 0.94 0.93 0.93 0.91* 0.93 0.94			

Table 2.14. Estimated coverage probabilities (ECP) of the bias-corrected percentile bootstrap (b = 500) interval of ρ_g estimated using ML. ECPs marked with an asterisk are significantly different from stated probabilities using a Type I error of 0.05.

					r							
					3	6		9				
					Stated	coverag	e proba	 bilitie	25			
Ha	H_{b}	ρg	n	0.80	0.95	0.80	0.95	0.80	0.95			
0.1	0.1	0.1	20 60	0.57*	0.71* 0.86*	0.69* 0.78	0.85* 0.96*	0.79	0.92*			
			100	0.72*	0.90*	0.75*	0.94	0.77*	0.94			
		0.5	20	0.66*	0.75*	0.77*	0.86*	0.83*	0.92*			
			60	0.79	0.88*	0.85*	0.95	0.81	0.95			
			100	0.82*	0.92*	0.82	0.95	0.77	0.94			
		0.9	20	0.72*	0.79*	0.83*	0.92*	0.84*	0.95			
			60	0.83*	0.92*	0.86*	0.97*	0.87*	0.96*			
			100	0.85*	0.96	0.87*	0.97*	0.89*	0.97*			
	0.5	0.1	20	0.69*	0.84*	0.79	0.94	0.80	0.95			
			60	0.73*	0.92*	0.78	0.94	0.78	0.93			
			100	0.74*	0.93	0.77*	0.94	0.77	0.93			
		0.5	20	0.76*	0.85*	0.84*	0.94	0.86*	0.95			
			60	0.85*	0.93	0.83*	0.95	0.80	0.94			
			100	0.84*	0.95	0.79	0.94	0.78	0.94			
		0.9	20	0.76*	0.87*	0.83*	0.97*	0.82*	0.96*			
			60	0.83*	0.95	0.89*	0.97*	0.89*	0.97*			
			100	0.87*	0.96*	0.90*	0.98*	0.90*	0.97*			

							r		
					3		6	9	
					Stated	coverag	e proba	bilitie	25
Ha	H _b	ρ _g	n	0.80	0.95	0.80	0.95	0.80	0.95
	0.9	0.1	20 60 100	0.69* 0.74* 0.77	0.83* 0.92* 0.94	0.78 0.79 0.77*	0.93* 0.94 0.93*	0.79 0.79 0.79	0.94 0.94 0.94
		0.5	20 60	0.77* 0.87*	0.83* 0.94	0.86* 0.85*	0.93* 0.96*	0.87* 0.78	0.96 0.93
		0.9	100 20 60 100	0.88* 0.79 0.87* 0.90*	0.96* 0.90* 0.96* 0.97*	0.80 0.85* 0.90* 0.91*	0.95 0.96* 0.97* 0.97*	0.78 0.85* 0.91* 0.91*	0.94 0.97* 0.97* 0.97*
0.5	0.5	0.1	20 60 100	0.77 0.79 0.79	0.93 0.94 0.94	0.78 0.78 0.80	0.92* 0.93 0.94	0.79 0.79 0.80	0.93* 0.94 0.94
		0.5	20 60 100	0.79 0.80 0.77 0.78	0.94 0.93* 0.93	0.78 0.77 0.79	0.94 0.93 0.93* 0.94	0.78 0.79 0.79	0.94 0.94 0.94 0.94
		0.9	20 60 100	0.80 0.82* 0.78	0.94 0.94 0.94	0.81 0.76* 0.76*	0.93* 0.93* 0.94	0.78 0.78 0.77	0.92* 0.93* 0.93*
	0.9	0.1	20 60 100	0.80 0.80 0.77	0.94 0.94 0.93*	0.79 0.79 0.80	0.94 0.95 0.95	0.79 0.78 0.80	0.93* 0.93* 0.95
		0.5	20 60 100	0.79 0.78 0.79	0.93* 0.93 0.93 0.93*	0.80 0.77* 0.81 0.78	0.95 0.92* 0.95 0.94	0.80 0.76* 0.79 0.79	0.95 0.91* 0.94 0.94
		0.9	20 60 100	0.81 0.77 0.77*	0.93 0.93* 0.93	0.77* 0.75* 0.77*	0.92* 0.91* 0.93*	0.76* 0.78 0.78	0.92* 0.94 0.93

					r							
					3	6		9				
					Stated	coverag	e proba	 bilitie	es			
Ha	H _b	ρ _g	n	0.80	0.95	0.80	0.95	0.80	0.95			
0.9	0.9	0.1 0.5 0.9	20 60 100 20 60 100 20 60 100	0.80 0.79 0.78 0.78 0.79 0.78 0.73* 0.76* 0.78	0.95 0.95 0.94 0.93 0.94 0.93 0.91* 0.92* 0.93*	0.79 0.79 0.80 0.79 0.80 0.78 0.73* 0.80 0.78	0.93 0.94 0.95 0.93 0.94 0.95 0.91* 0.94 0.94	0.80 0.79 0.79 0.79 0.78 0.78 0.75* 0.78 0.78	0.94 0.94 0.94 0.93 0.93 0.91* 0.93 0.94			

Table 2.15. Estimated lengths of the bias-corrected percentile bootstrap (b = 500) intervals of ρ_g estimated using MANOVA and ML (1 - α = 0.95).

			n			r			
					MANOV	'A	ML		
H _a	H_{b}	ρ _g		3	6	9	3	6	9
0.1	0.1	0.1	20 60	7.85	5.92 2.46	4.43	1.69	1.75	1.70
			100	4.20	1.49	0.91	1.57	1.44 1.17	0.88
		0.5	20	7.24	5.47	3.69	1.71	1.67	1.59
			60	4.81	2.14	1.26	1.59	1.29	1.01
			100	3.50	1.27	0.76	1.47	1.00	0.73
		0.9	20	6.95	4.98	3.33	1.64	1.52	1.29
			60	4.87	2.22	1.09	1.43	0.94	0.56
			100	3.81	1.26	0.59	1.25	0.60	0.34
	0.5	0.1	20	4.03	2.68	2.00	1.64	1.59	1.47
			60	2.01	1.15	0.86	1.36	1.07	0.85
		_	100	1.51	0.80	0.61	1.16	0.78	0.61
		0.5	20	3.58	2.49	1.90	1.62	1.50	1.36
			60	1.96	1.14	0.76	1.29	0.94	0.71
		• •	100	1.45	0.73	0.52	1.08	0.68	0.52
		0.9	20	3.61	2.48	1.83	1.54	1.31	1.08
			60	2.33	1.22	0.67	1.16	0.64	0.37
			100	1.96	0.73	0.39	0.94	0.38	0.24
	0.9	0.1	20	2.84	2.29	1.86	1.44	1.42	1.35
			60	1.75	1.05	0.82	1.20	0.96	0.80
			100	1.22	0.74	0.57	1.00	0.72	0.57
		0.5	20	2.85	2.26	1.78	1.40	1.32	1.22
			60	1.92	1.08	0.74	1.14	0.87	0.69
			100	1.48	0.73	0.50	0.98	0.65	0.50
		0.9	20	3.16	2.54	1.91	1.33	1.16	0.97
			60	2.46	1.24	0.70	1.07	0.60	0.37
			100	2.01	0.78	0.39	0.86	0.38	0.23

				r							
					MANOV	'A		ML			
Ha	H _b	ρ _g	n	3	6	9	3	6	9		
0.5	0.5	0.1	20 60 100	1.55 0.68 0.52	1.07 0.58 0.44	0.97 0.54 0.42	1.28 0.68 0.52	1.05 0.58 0.44	0.97		
		0.5	20 60	1.29 0.55	0.89 0.46	0.79 0.42	1.10 0.55	0.88 0.46	0.42 0.79 0.42		
		0.9	100 20 60 100	0.41 0.91 0.27 0.20	0.35 0.40 0.17 0.13	0.33 0.30 0.15 0.11	0.41 0.56 0.23 0.18	0.35 0.31 0.17 0.13	0.33 0.27 0.14 0.11		
	0.9	0.1	20 60 100	1.13 0.58 0.45	0.94	0.90	1.08	0.94 0.53	0.90		
		0.5	20 60 100	0.45 0.96 0.47 0.36	0.41 0.76 0.42 0.32	0.40 0.73 0.41 0.31	0.45 0.90 0.47 0.36	0.41 0.76 0.42 0.32	0.40 0.73 0.41 0.31		
		0.9	20 60 100	0.58 0.20 0.15	0.32 0.14 0.11	0.26 0.13 0.09	0.38 0.40 0.18 0.14	0.32 0.27 0.14 0.11	0.31 0.25 0.13 0.09		
0.9	0.9	0.1	20 60 100	0.87 0.50 0.39	0.84 0.49 0.38	0.84 0.49 0.38	0.87 0.50 0.39	0.84 0.49 0.38	0.84 0.49 0.38		
		0.5	20 60 100	0.69 0.39 0.31	0.68 0.38 0.30	0.67 0.38	0.69 0.39	0.68 0.38	0.67 0.38		
		0.9	20 60 100	0.23 0.12 0.09	0.21 0.11 0.08	0.29 0.20 0.10 0.08	0.31 0.23 0.12 0.09	0.30 0.21 0.11 0.08	0.29 0.20 0.10 0.08		

References

- Amemiya, Y (1985). What should be done when an estimated between-group covariance matrix is not nonnegative definite? The American Statistician 39:112-117.
- Anderson, R. L. and P. P. Crump (1967). Comparisons designs and estimation procedures for estimating parameters in a two-stage nested process. Technometrics 9:499-516.
- Arvesen, J. N. and T. H. Schmitz (1970). Robust procedures for variance component problems using jackknife. Biometrics 26:677-686.
- Bridges, W.C., Knapp, S.J., and Cornelius, P.J. 1990. Standard errors and confidence interval estimators for expected selection response. Crop Science (in press).
- Efron, B (1982). The Jackknife, the Bootstrap and other resampling plans. Philadelphia:SIAM.
- Efron, B (1987). The better bootstrap confidence intervals. Journal of the American Statistical Association, 82:171- 185.
- Efron, B. and R. Tibshirani (1986). Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Science 1:54-77.
- Falconer, D. S. (1981). Introduction to quantitative genetics. Edition 2. Longman, London.

- Klotz, J. and J. Putter (1969). Maximum likelihood estimation of multivariate covariance components for the balanced one-way layout. The Annals of Mathematical Statistics 40:1100-1105.
- Knapp, S. J. and W. C. Bridges, Jr. (1988). Parametric and jackknife confidence interval estimators for two-factor mating design genetic variance ratios. Theoretical and Applied Genetics 76:385-392.
- Knapp, S. J., W. C. Bridges, Jr. and M. H. Yang (1989). Nonparametric confidence interval estimators for heritability and expected selection response. Genetics 121:891-898.
- Knapp, S. J., Tagliani, L. A., and Liu, B.-H. (1991). Outcrossing rates of experimental populations of Cuphea lanceolata. Crop Science. (in review).
- McCutchan, B. G., J. X. Ou, and G. Namkoong (1985). A comparison of planned unbalanced designs for estimating heritability in perennial tree crops. Theoretical and Applied Genetics 71:536-544.
- Miller, R. G. (1974). The jackknife-a review. Biometrika 61:115.
- Mitchell-old, T. and J. Bergelson (1990). Statistical genetics of Impatiens capensis. I. Genetic basis of quantitative variation. Genetics 124:407-415.
- Reeve, E. C. R. (1955). The variance of the genetic correlation coefficient. Biometrics 11:357-374.

- Riska, B., T. Prout and M. Turelli (1989). Laboratory estimates of heritabilities and genetic correlations in nature. Genetics 123:865-871.
- Robertson, A (1959). The sampling variance of the genetic correlation. Biometrics 15:469-485.
- Scheinberg, E (1966). The sampling variance of the correlation coefficients estimated in genetic experiments. Biometrics 22:187-191.
- Schenker, N. (1985). Qualms about bootstrap confidence intervals. Journal of the American Statistical Association 80:360-361.
- Schoen, D. J. and M. T. Clegg (1986). Monte Carlo studies of plant mating system estimation models: the onepollen parent and mixed mating models. Genetics 112:927-945.
- Tallis, G. M. (1959). Sampling errors of genetic correlation coefficients calculated from the analysis of variance and covariance. Aust. Jour. of Stat. 1:35-43.
- Thompson, W. O. (1975). A comparison of designs and estimators for the two-stage nested random model. Technometrics 17:37-44.

BIBLIOGRAPHY

- Amemiya, Y (1985). What should be done when an estimated between-group covariance matrix is not nonnegative definite? The American Statistician 39:112-117.
- Anderson, R. L. and P. P. Crump (1967). Comparisons designs and estimation procedures for estimating parameters in a two-stage nested process. Technometrics 9:499-516.
- Arvesen, J. N. and T. H. Schmitz (1970). Robust procedures for variance component problems using jackknife. Biometrics 26:677-686.
- Baker, R. J. (1986). Selection indices in plant breeding. CRC Press, Inc. Boca Raton, Florida.
- Bridges, W.C., Knapp, S.J., and Cornelius, P.J. 1990. Standard errors and confidence interval estimators for expected selection response. Crop Science (in press).
- Efron, B (1982). The Jackknife, the Bootstrap and other resampling plans. Philadelphia:SIAM.
- Efron, B (1987). The better bootstrap confidence intervals. Journal of the American Statistical Association, 82:171-185.
- Efron, B. and R. Tibshirani (1986). Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Science 1:54-77.
- Falconer, D. S. (1981). Introduction to quantitative genetics. Edition 2. Longman, London.

- Hill, W. G. and R. Thompson (1978). Probabilities of nonpositive definite between-group or genetic covariance matrices. Biometrics 34:429-439.
- Harville, D. A. (1977). Maximum likelihood approaches to variance component estimation and to related problems. Journal of the American Statistical Association. 72:320-338.
- Henderson, C. R. (1984). Applications of linear models in animal breeding. University of Guelph, Guelph, Ontario, Canada.
- Johnson, M. E. (1987). Multivariate statistical simulation. John Wiley & Son, New York.
- Kinderman, A. J. (1975). Computer generation of random variables with normal and Studnet's T distributions. In: Proceedings of the statistical computing section, The American Statistical Association.
- Klotz, J. and J. Putter (1969). Maximum likelihood estimation of multivariate covariance components for the balanced one-way layout. The Annals of Mathematical Statistics 40:1100-1105.
- Knapp, S. J. and W. C. Bridges, Jr. (1988). Parametric and jackknife confidence interval estimators for two-factor mating design genetic variance ratios. Theoretical and Applied Genetics 76:385-392.

- Knapp, S. J., W. C. Bridges, Jr. and M. H. Yang (1989). Nonparametric confidence interval estimators for heritability and expected selection response. Genetics 121:891-898.
- Knapp, S. J., Tagliani, L. A., and Liu, B.-H. (1991). Outcrossing rates of experimental populations of Cuphea lanceolata. Crop Science. (in review).
- Lande, R. (1984). The genetic correlation between characters maintained by selection, linkage and inbreeding. Genetic Research 44:309-320.
- Liu, B. H. and S. J. Knapp (1991) Statistical properties of MANOVA, REML, and ML estimators of genetic correlation coefficient. In review.
- McCutchan, B. G., J. X. Ou, and G. Namkoong (1985). A comparison of planned unbalanced designs for estimating heritability in perennial tree crops. Theoretical and Applied Genetics 71:536-544.
- Miller, R. G. (1974). The jackknife-a review. Biometrika 61:115.
- Mitchell-old, T. and J. Bergelson (1990). Statistical genetics of Impatiens capensis. I. Genetic basis of quantitative variation. Genetics 124:407-415.
- Rao, C. R. and J. Kleffe (1988). Estimation of variance components and applications. North-Holland, Amsterdam.
- Reeve, E. C. R. (1955). The variance of the genetic correlation coefficient. Biometrics 11:357-374.

- Riska, B., T. Prout and M. Turelli (1989). Laboratory estimates of heritabilities and genetic correlations in nature. Genetics 123:865-871.
- Robertson, A (1959). The sampling variance of the genetic correlation. Biometrics 15:469-485.
- Scheinberg, E (1966). The sampling variance of the correlation coefficients estimated in genetic experiments. Biometrics 22:187-191.
- Schenker, N. (1985). Qualms about bootstrap confidence intervals. Journal of the American Statistical Association 80:360-361.
- Schoen, D. J. and M. T. Clegg (1986). Monte Carlo studies of plant mating system estimation models: the one-pollen parent and mixed mating models. Genetics 112:927-945.
- Searle, S. R. (1970) Linear Models. John Wiley & Sons, New York.
- Swallow, W. H. and J. F. Monahan (1984). Monte Carlo comparison of ANOVA, MIVQUE, REML, and ML estimators of variance components. Technometrics 26:47-57.
- Tallis, G. M. (1959). Sampling errors of genetic correlation coefficients calculated from the analysis of variance and covariance. Aust. Jour. of Stat. 1:35-43.
- Thompson, W. O. (1975). A comparison of designs and estimators for the two-stage nested random model. Technometrics 17:37-44.

VanVleck, L. D. and C. R. Henderson (1961). Empirical sampling estimates of genetic correlations. Biometrics 17:359-371.