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Probabilities of negative estimates of genetic variances*

W. C. Bridges Jr. [1] **and S. J. Knapp** [2]

[1] Experimental Statistics Unit, Clemson University, Clemson, SC 29634, USA
[2] Department of Crop Science, Oregon State University, Corvallis, OR 97331, USA

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Summary. The probability of negative analysis of variance estimates of genetic variance components due to sampling error (Ps) was investigated. The objectives were to evaluate the magnitude of Ps, to compare Ps for estimates of σ_A^2 and σ_D^2, and to compare Ps for genetic variance component estimates from the nested and factorial mating designs. Ps was defined in terms of ratios of mean squares and the F distribution was used to calculate probabilities of the negative estimates. The results indicated that Ps is often greater than 0.20 for σ_D^2. It is generally lower for σ_A^2 than for σ_D^2, and lower for the factorial mating design than the nested mating design.

Key words: Genetic variance component estimation – Nested mating design – Factorial mating design

Introduction

The nested (Design 1) and factorial (Design 2) mating designs are useful for obtaining estimates of the genetic variance components due to breeding values (σ_A^2) and dominance deviations (σ_D^2) (Comstock and Robinson 1948; Hallauer and Miranda 1981). The analysis of variance (ANOVA) method is often used to calculate these estimates of genetic variances (Hallauer and Miranda 1981). ANOVA estimators have the advantages of being unbiased and having minimum variance among all unbiased quadratic estimators, but also have the disadvantage of the possibility of negative estimates of the variance components (Hallauer and Miranda 1981; Searle 1971).

The occurrence of negative estimates of genetic variance components has been reported many times in the literature (ElRouby and Penny 1967; Leone et al. 1968; Lindsey et al. 1962; Robinson et al. 1955; Sentz 1971; Williams et al. 1965). The negative estimates are usually attributed to some combination of an inadequate genetic model (no epistatic effects in the model), sampling error, inadequate experiment design (competition effects among the individuals), and assortative mating (Hallauer and Miranda 1981; Lindsey et al. 1962). The true magnitude of the probability of negative estimates is not clear from these reports. The reports do suggest that negative estimates of σ_D^2 are more frequent than negative estimates of σ_A^2 and that negative estimates of both genetic variance components from the nested mating design are more frequent than negative estimates of genetic variance components from the factorial mating design.

The purpose of this research was to study the probability of obtaining negative ANOVA estimates of genetic variance components due to sampling error (Ps) only. The specific objectives were to evaluate the magnitude of Ps in general, and to compare Ps for σ_A^2 and σ_D^2 and for nested and factorial mating designs.

Materials and methods

Derivation of probabilities

The analysis of variance for a nested mating design in a replications-in-sets experiment design is shown in Table 1. Random design factors, balanced data, no competition effects, no epistasis, normal diploid meiosis, no linkage, two alleles per locus, non-inbred material, and random mating were assumed. The ANOVA estimators of the genetic variance components

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are

$$\hat{\sigma}_A^2 = 4\,[(M_M - M_{F(M)})/fr] = 4\,\hat{\sigma}_M^2 \quad (1)$$

and

$$\hat{\sigma}_D^2 = 4\,[(M_{F(M)} - M_R)/r - (M_M - M_{F(M)})fr] = 4\,[\hat{\sigma}_{F(M)}^2 - \hat{\sigma}_M^2] \quad (2)$$

where terms are defined in Table 1.

The analysis of variance for a factorial mating design in a replications-in-sets experiment design is shown in Table 2. Assumptions were analogous to Table 1. The ANOVA estimators of the genetic variance components are (using a pooled estimator of $\hat{\sigma}_A^2$)

$$\hat{\sigma}_A^2 = 2\,[(M_M - M_{MF})/rf + (M_F - M_{MF})/rm] = 2\,[\hat{\sigma}_M^2 + \hat{\sigma}_F^2] \quad (3)$$

and

$$\hat{\sigma}_D^2 = 4\,[(M_{MF} - M_R)/r] = 4\,\hat{\sigma}_{MF}^2 \quad (4)$$

where terms are defined in Table 2.

Four probabilities were derived based on the methods of Leone et al. (1968) and Gill and Jensen (1968). The following notation was used for these probabilities:

Psan = probability of negative ANOVA estimates of σ_A^2 from the nested mating design
Psdn = probability of negative ANOVA estimates of σ_D^2 from the nested mating design
Psaf = probability of negative ANOVA estimates of σ_A^2 from the factorial mating design
Psdf = probability of negative ANOVA estimates of σ_D^2 from the factorial mating design

Psan is equivalent to the probability that M_M is less than $M_{F(M)}$ in (1). Therefore Psan can be written

$$\text{Psan} = P\{M_M < M_{F(M)}\} = P\{M_M/M_{F(M)} < 1\}.$$

If the measured trait is normally distributed, then the random variable

$$\text{Fsan} = [M_M/E(M_M)]/[M_{F(M)}/E(M_{F(M)})]$$

has an F distribution with df_M and $df_{F(M)}$ degrees of freedom and Psan can be written in terms of Fsan as follows:

$$\text{Psan} = P\{[M_M/E(M_M)]/[M_{F(M)}\,E(M_{F(M)})] < E(M_{F(M)})/E(M_M)\} = P\{\text{Fsan} < E(M_{F(M)})/E(M_M)\}.$$

Psdf is equivalent to the probability that M_{MF} is less than M_R in (4). Psdf can be written in terms of an F-statistic similar to Psan as follows:

$$\text{Psdf} = P\{\text{Fsdf} < E(M_R)/E(M_{MF})\}$$

where Fsdf is a random variable that has an F distribution with df_{MF} and df_R degrees of freedom.

Psdn is equivalent to the probability that $(f+1)\,M_{F(M)}$ is less than $(f\,M_R + M_M)$ in (2). Therefore Psdn can be written

$$\text{Psdn} = P\{(f+1)\,M_{FM} < fM_R + M_M\} = P\{M_{F(M)}/[fM_R + M_M] < (f+1)^{-1}\}.$$

If the measured trait is normally distributed, then the random variable

$$\text{Fsdn} = [M_{F(M)}/E(M_{F(M)})]/[(fM_R + M_M)/(fE(M_R) + E(M_M))]$$

has an approximate F distribution with $df_{F(M)}$ and $(fE(M_R) + E(M_M))^2/(((fE(M_R))^2/df_R) + ((E(M_R)^2)/df_M))$ degrees of freedom (Satterthwaite 1946; Searle 1971) and Psdn can be written in terms of Fsdn as follows:

$$\text{Psdn} = P\{[M_{F(M)}/E(M_{F(M)})]/[(fM_R + M_M)/(fE(M_R) + E(M_M))] < [fE(M_R) + E(M_M)]/[(f+1)\,E(M_{F(M)})]\} = P\{\text{Fsdn} < [fE(M_R) + E(M_M)]/[(f+1)\,E(M_{F(M)})]\}.$$

Psaf is equivalent to the probability that $(m\,M_M + f\,M_F)$ is less than $(m + f)\,M_{MF}$ in (3). Psaf can be written in terms of an F-statistic similar to Psdn as follows:

$$\text{Psaf} = P\{\text{Fsaf} < [(m+f)\,E(M_{MF})]/[fE(M_F) + mE(M_M)]\}$$

where Fsaf is a random variable that has an approximate F distribution with $(mE(M_M) + fE(M_F))^2/(((mE(M_M))^2/df_M) + ((fE(M_F))^2/df_F))$ and df_{MF} degrees of freedom (Satterthwaite 1946; Searle 1971).

The derived probabilities are functions of the expected mean squares. The expected mean squares are functions of the variance components and the design factors (see Tables 1 and 2). Values were assigned to each variance component and design factor so that the probabilities could studied. The values were chosen to approximate actual mating design experiment conditions and were as follows:

Variance component	Assigned value(s)
σ_A^2	1, 2, 3, 4
σ_D^2	0.25, 0.5, 0.75, 1
σ_{EB}^2	1.5
σ_{EW}^2	0.25
Design factor	**Assigned value(s)**
sets	1, 2
males	5, 10
females	5, 10
replications	2, 4
individuals	20

The values of σ_A^2 and σ_D^2 were chosen so that the effect of the genetic variance magnitude on Ps could be studied. The values for number of sets, males, females, and replications were chosen so that the effect of allocation on Ps could be studied. The values of the variance components and design factors were used to define 256 different combinations that represent different mating experiments. The four probabilities were calculated in each experiment.

Results

The means, medians, maximum values, and minimum values of the four probabilities across all 256 experiments are shown in Table 3. The means of the four probabilities were contrasted to compare Ps for the nested and factorial mating designs and for σ_D^2 and σ_A^2. The contrast of the means of Psan and Psaf (0.0431 vs 0.0059) indicated that Ps for σ_A^2 is less in the factorial mating design than in the nested mating design. The

Table 1. Analysis of variance for a nested mating design in a replications-in-sets experiment design

Source of variation[a]	Degrees of freedom[b,c]	Mean square[c]	Expectation of mean square
			Observational[c,d]
S			
B(S)			
M(S)	$df_M = s(m-1)$	M_M	$E(M_M) = \sigma^2_R + r\,\sigma^2_{F(M)} + f\,r\,\sigma^2_M$
F(MS)	$df_{F(M)} = s\,m(f-1)$	$M_{F(M)}$	$E(M_{F(M)}) = \sigma^2_R + r\,\sigma^2_{F(M)}$
R	$df_R = s(m\,f-1)(r-1)$	M_R	$E(M_R) = \sigma^2_R$
Genetic[c,e]			
			$E(M_M) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB} + r(\frac{1}{4}\sigma^2_A + \frac{1}{4}\sigma^2_D) + f\,r(\frac{1}{4}\sigma^2_A)$
			$E(M_{F(M)}) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB} + r(\frac{1}{4}\sigma^2_A + \frac{1}{4}\sigma^2_D)$
			$E(M_R) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB}$

[a] S: sets; B: blocks; M: males; F: females; R: pooled residual
[b] s: number of sets; m: number males/set; f: number of females/males/set; r: number of replications; k: number of individuals/plot
[c] The S has been omitted from subscripts to simplify notation
[d] σ^2_R: pooled residual variance component; $\sigma^2_{F(M)}$: female-within-male-set combination variance component; σ^2_M: male-within-set variance component
[e] σ^2_{EW} and σ^2_{EB}: variance components due to environmental variance within and between plots, respectively; σ^2_A and σ^2_D: variance components due to breeding values and dominance deviations, respectively

Table 2. Analysis of variance for a factorial mating design in a replications-in-sets experiment design

Source of variation[a]	Degrees of freedom[b,c]	Mean square[c]	Expectation of mean square
			Observational[c,d]
S			
B(S)			
M(S)	$df_M = s(m-1)$	M_M	$E(M_M) = \sigma^2_R + r\,\sigma^2_{MF} + r\,f\,\sigma^2_M$
F(S)	$df_F = s(f-1)$	M_F	$E(M_F) = \sigma^2_R + r\,\sigma^2_{MF} + r\,m\,\sigma^2_F$
M × F(S)	$df_{MF} = s(m-1)(f-1)$	M_{MF}	$E(M_{MF}) = \sigma^2_R + r\,\sigma^2_{MF}$
R	$df_R = s(m\,f-1)(r-1)$	M_R	$E(M_R) = \sigma^2_R$
Genetic[c,e]			
			$E(M_M) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB} + r(\frac{1}{4}\sigma^2_D) + r\,f(\frac{1}{4}\sigma^2_A)$
			$E(M_F) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB} + r(\frac{1}{4}\sigma^2_D) + r\,m(\frac{1}{4}\sigma^2_A)$
			$E(M_{MF}) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB} + r(\frac{1}{4}\sigma^2_D)$
			$E(M_R) = (\sigma^2_{EW} + \frac{1}{2}\sigma^2_A + 3/4\,\sigma^2_D)/k + \sigma^2_{EB}$

[a] S: sets; B: blocks; M: males; F: females; R: pooled residual
[b] s: number of sets; m: number of males/set; f: number of females/male/set; r: number of replications; k: number of individuals/plot
[c] The S has been omitted from subscripts to simplify notation
[d] σ^2_R: pooled residual variance component; σ^2_{MF}: male-female interaction variance component; σ^2_F: female variance component; σ^2_M: male variance component
[e] σ^2_{EW} and σ^2_{EB}: variance components due to environmental variance within and between plots, respectively; σ^2_A and σ^2_D: variance components due to breeding values and dominance deviations, respectively

contrast of the means of Psdn and Psdf (0.3501 vs 0.1946) indicated that Ps for σ_D^2 is less in the factorial mating design than in the nested mating design. The comparison of Ps for the two mating designs is similar for σ_A^2 and σ_D^2. These comparisons indicate that Ps is generally less for the factorial mating design than for the nested mating design. The contrast of the means of Psan and Psdn (0.0431 vs 0.3501) indicated that Ps for σ_A^2 is less than Ps for σ_D^2 for the nested mating design. The contrast of the means of Psaf and Psdf (0.0059 vs 0.1946) indicated that Ps for σ_A^2 is also less than Ps for σ_D^2 for the factorial mating design. The comparison of Ps for σ_A^2 and σ_D^2 is similar for both mating designs. These comparisons indicate that Ps is generally less for σ_A^2 than for σ_D^2.

The same conclusions can be reached by contrasting the medians of Psan, Psdn, Psaf, and Psdf from Table 3. The contrast of the medians of Psan and Psaf (0.0217 vs 0.0001) along with the contrast of Psdn and Psdf (0.3670 vs 0.1911) indicate that Ps is generally less for the factorial mating design. The contrast of the medians of Psan and Psdn (0.0217 vs 0.3670) along with the contrast of Psaf and Psdf (0.0001 vs 0.1911) indicate that Ps is generally less for σ_A^2 than for σ_D^2.

The maximum and minimum values of the four probabilities from Table 3 indicate that the magnitude of Ps could be much larger than expected for σ_D^2 in some experiments (Psdn = 0.4568) and negligible for σ_A^2 in other experiments (Psan = 0.0000 and Psaf = 0.0000). The logical next step was to determine the frequency of experiments in which large Ps values occur. The means and medians from Table 3 suggest that large Ps occur often for σ_D^2.

Frequency tables for the four probabilities are shown in Table 4. Psan and Psaf values less than 0.10 occurred in 84.8% and 98.8% of the experiments, respectively. Psdn and Psdf values greater than 0.20 occurred in 94.5% and 47.3% of the experiments respectively. These frequencies indicate that large Ps values for σ_D^2 are common in the experiments considered while large Ps values for σ_A^2 are rare.

The combined data in Tables 3 and 4 show that Psdn had the highest mean and median and the highest concentration of Ps values greater than 0.20. Psaf had the lowest mean and median and the highest concentration of Ps values less than 0.10. We can conclude that estimating σ_D^2 from the nested mating design involved the highest general Ps and that estimating σ_A^2 from the factorial mating design involved the lowest general Ps. This conclusion follows from the comparisons of Ps for the nested and factorial mating designs and σ_D^2 and σ_A^2.

The effect of genetic variance component magnitude on Ps was evaluated to determine if the relatively large Ps values occurred only in experiments with relatively small values of the genetic variance components. Psan and Psaf values were averaged over all experiments with a particular value of σ_A^2 (Table 5). The mean Psan and Psaf increased as the value of σ_A^2 decreased, but the mean Psan and Psaf were less than 0.10 for even the smallest value of σ_A^2. Psdn and Psdf values were also averaged over all experiments with a particular value of σ_D^2 (Table 5). The mean Psdn and Psdf increased as the value of σ_D^2 decreased and were greater than 0.30 for the smallest value of σ_D^2. However, the mean Psdn was greater tan 0.25 for even the largest value of σ_D^2 and Psdf was greater than 0.10 for all but the largest value of σ_D^2. These data indicate that negative estimates of σ_D^2 can occur for the largest and the smallest values of σ_D^2.

Table 3. Means, medians, maximum values, and minimum values of the probabilities of negative estimates of genetic variances due to sampling error (Ps)

	Ps[a]			
	Psan	Psdn	Psaf	Psdf
Mean	0.0431	0.3501	0.0059	0.1946
Median	0.0217	0.3670	0.0001	0.1911
Maximum	0.2691	0.4568	0.1292	0.4485
Minimum	0.0000	0.0552	0.0000	0.0001

[a] Psan and Psdn are the probabilities of negative estimates of breeding value and dominance deviation genetic variances, respectively, from the nested mating design; Psaf and Psdf are the probabilities of negative estimates of breeding value and dominance deviation genetic variances, respectively, from the factorial mating design

Table 4. Frequency tables for the probabilities of negative estimates of genetic variances due to sampling error (Ps)

Class	Ps[a]			
	Psan	Psdn	Psaf	Psdf
$0 \leq Ps < 0.1$	217[b]	1	253	78
	84.8	0.4	98.8	30.5
$0.1 < Ps < 0.2$	35	13	3	57
	13.3	5.1	1.2	22.3
$0.2 < Ps < 0.3$	5	42	0	53
	2.0	16.4	0	20.7
$0.3 < Ps < 0.4$	0	119	0	52
	0	46.5	0	20.3
$0.4 < Ps \leq 1.0$	0	81	0	16
	0	31.6	0	6.3

[a] Psan, Psdn, Psaf, and Psdf are defined in Table 3

[b] Top number is the absolute frequency of experiments with a Ps value in the particular class; Bottom number is the percentage (out of 256) of the experiments with a Ps value in the particular class

Table 5. Mean probabilities of negative estimates of genetic variance due to sampling error (Ps) for different values of the genetic variance components

Genetic[a] variance	Value of genetic variance	Ps[b]	
		Psan	Psaf
σ_A^2	1	0.0781	0.0181
	2	0.0410	0.0037
	3	0.0294	0.0013
	4	0.0239	0.0005
		Psdn	Psdf
σ_D^2	0.25	0.4222	0.3272
	0.50	0.3696	0.2107
	0.75	0.3239	0.1416
	1.00	0.2846	0.0988

[a] σ_A^2 and σ_D^2 are the variance components due to breeding values and dominance deviations, respectively
[b] Psan, Psaf, Psdn, and Psdf are defined in Table 3

Table 6. Mean probabilities of negative estimates of genetic variance due to sampling error (Ps) for different combinations of values of sets, males, females, and replications

Combination	Design factor value[a]				Ps[b]			
	s	m	f	r	Psan	Psaf	Psdn	Psdf
1	1	5	5	2	0.1685	0.0423	0.4160	0.3661
2	1	5	5	4	0.1236	0.0154	0.3852	0.2508
3	1	5	10	2	0.0788	0.0091	0.3796	0.2984
4	1	5	10	4	0.0512	0.0020	0.3480	0.1541
5	1	10	5	2	0.0599	0.0091	0.3919	0.2984
6	1	10	5	4	0.0317	0.0020	0.3577	0.1541
7	1	10	10	2	0.0130	0.0004	0.3478	0.2202
8	1	10	10	4	0.0051	0.0000	0.3143	0.0788
9	2	5	5	2	0.0714	0.0107	0.3921	0.3076
10	2	5	5	4	0.0402	0.0020	0.3587	0.1663
11	2	5	10	2	0.0179	0.0009	0.3501	0.2291
12	2	5	10	4	0.0077	0.0001	0.3177	0.0867
13	2	10	5	2	0.0147	0.0009	0.3551	0.2291
14	2	10	5	4	0.0045	0.0001	0.3158	0.0867
15	2	10	10	2	0.0010	0.0000	0.3030	0.1489
16	2	10	10	4	0.0001	0.0000	0.2980	0.0374

[a] s: number of sets; m: number of males; f: number of females; r: number of replications
[b] Psan, Psaf, Psdn, and Psdf are defined in Table 3

The effect of genetic variance component magnitude on Ps was also evaluated to determine if the difference in Ps for σ_A^2 and σ_D^2 was due to the different ranges of values for σ_A^2 and σ_D^2. The four probabilities were recalculated using values of 1, 2, 3, and 4 for both σ_A^2 and σ_D^2. The means of Psan, Psdn, Psaf, and Psdf were 0.0682, 0.1643, 0.0167, and 0.0368, respectively. The comparisons of Ps for σ_A^2 and σ_D^2 do not change. The difference in Ps for σ_A^2 and σ_D^2 seems to be due to the method of estimation rather than the magnitude of the variance components.

The effect of design factor magnitude on Ps was evaluated to determine if the relatively large Ps values occurred only in relatively small sized experiments, i.e., experiments with small values of the design factors. Ps values were averaged for all possible combinations of design factor values (Table 6). The mean Psan is greater than 0.10 only for the smallest experiment sizes (combinations 1 and 2), while the mean Psaf is less than 0.10 for all experiment sizes. The mean Psdn is greater than 0.25 for all experiment sizes and the mean Psdf is greater than 0.10 for all but the largest experiment sizes (combinations 8, 12, 14, and 16). These data indicate that negative estimates of σ_D^2 occur frequently for even the largest experiment sizes.

The results are summarized as follows: (1) Ps is less for σ_A^2 than for σ_D^2; (2) Ps is less for the factorial mating design than for the nested mating design; (3) Ps for σ_D^2 can be 0.20 and greater in many of the mating experiments considered; (4) the largest Ps values occur when estimating σ_D^2 from the nested mating design and the smallest occur when estimating σ_A^2 from the factorial mating design; (5) Ps for σ_D^2 can be 0.20 and greater for even the largest experiment sizes and values of σ_D^2 considered.

Discussion

Negative estimates of genetic variance components are difficult to interpret (Searle 1971) and therefore undesirable in mating design experiments. The high values of Ps indicate that negative estimates are a significant problem in mating design experiments. The results of our research suggest three methods to reduce the probability of negatives estimates occurring.

The first method to reduce Ps is to use the factorial mating design instead of the nested mating design. The nested mating design is presently used more frequently (Hallauer and Miranda 1981) because the matings are often easier to achieve. However the higher Ps for the nested design in our study indicates the more difficult factorial matings should be attempted whenever possible. This recommendation agrees with Comstock and Robinson (1952) who reported that the nested matign design gives less precise estimates for σ_D^2. The probability of negative estimates of σ_D^2 is still relatively large even in the factorial mating design (Table 5).

The second method is to use the data in Table 6 to determine the best allocation of design factor resources to reduce Ps. For example, consider an experiment where the objective is to estimate σ_D^2 and the factorial mating design is used. Obviously combination 16 (the

largest experiment size) has the minimum Psdf and combination 1 (the smallest experiment size) has the maximum Psdf. Suppose that the resources are not available for the largest experiment. Resources are available for an experiment with one set, five males, five females, and four replications (combination 2) or an experiment with two sets, five males, five females, and two replications (combination 9). The values of Psdf (0.2508 vs 0.3076) indicate that the combination 2 experiment is better for reducing Ps. If the objective was to estimate σ_A^2, the values of Psaf (0.0154 vs 0.0107) indicate that the combination 9 experiment is preferable. If the objective was to estimate both σ_A^2 and σ_D^2, then the combination 2 experiment is preferable because both values of Psaf are relatively small compared to the values of Psdf.

A table similar to Table 6 can be constructed to study allocation for almost any mating design experiment of interest by modifying the calculation of Ps. Different values of the variance components and design factors can be substituted into the calculation of Ps to reflect realistic values for the specific experiment of interest. If the experiment design is completely randomized rather than a randomized block, then the source of variation for block in Tables 1 and 2 would be removed and the pooled residual degrees of freedom becomes $(smf)(r-1)$. The new degrees of freedom can be substituted into the calculation of Ps. If the unit of the experiment is an individual rather than a plot then $k = 1$ and $\sigma_{EW}^2 = 0$. These new values can be used in the calculation of Ps. These modifications of the calculation of Ps will change the overall magnitude of Ps but should not change the comparisons.

The third method is to use estimators other than ANOVA to estimate the genetic variance components. Maximum likelihood estimators (Hayman 1960) are often suggested as an alternative. These estimators are biased but the probability of negative estimates is zero. The maximum likelihood estimation method will not solve the problem of negative estimates of σ_D^2 from the nested mating design unless the maximum likelihood estimate is derived for $\hat{\sigma}_D^2$. If the maximum likelihood estimates (Searle 1971) of σ_M^2 and $\sigma_{F(M)}^2$ are simply substituted into (2), the estimate could still be negative.

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