MANUAL OF PROCEDURES IN QUANTITATIVE GENETICS

SECOND EDITION

Walter A. Becker
Associate Professor of Genetics
Washington State University

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PREFACE TO FIRST EDITION

This manual was written during the teaching of a course in quantitative genetics at Washington State University and was designed to present many of the basic procedures used in quantitative genetics. An attempt has been made to cover areas applicable to both plant and animals.

Within each procedure the statistical model is given first, and then the genetic meaning of the various components of the model. The statistical formulas for computing the procedures are presented with a worked example. Throughout the manual the dot notation has been utilized in the formulas. Occasionally an example is omitted because a previous example can suffice or because suitable data were not available. References are made throughout to more advanced or other procedures that might be of use to the student or researcher.

Tables are provided at the end of the manual for ready reference. Standard statistical tables (such as the t or F tables) were not included because they are readily available in other books. Books whose subject matter bears upon population and quantitative genetics have been listed for the information of the reader.

The author is indebted to the classes in quantitative genetics whose members constructed Table 3, worked the examples, and contributed many constructive suggestions. Appreciation is expressed to Dr. Thomas Bogyo who recommended the use of the augmented matrix and assisted in, as did Dr. Surendra Sinha, the preparation of portions of the section on selection indexes. Dr. James Hanover, of the Forest Services Laboratory, Moscow, Idaho, kindly furnished the data of the factorial cross.

Walter A. Becker
August, 1964
Pullman, Washington

PREFACE TO SECOND EDITION

The first edition of this manual has been extensively rewritten, with more explanatory text and distinct divisions made between plant and animal designs in each section. Table 2 (formerly table 3) has been expanded to include populations up to 400.

Grateful acknowledgment is given to Benjamin Hawkes, who was responsible for the calculations involving the expansion of table 2 and to several persons who suggested improvements and corrections.

Walter A. Becker
August, 1967
Pullman, Washington

SYMBOLS

The statistical symbols in this booklet will follow, in general, those in Federer (1955, pp. 16-17). Dot notation is used throughout.

I. Statistical symbols

Symbol	Meaning
X_i or Y_i	the i^{th} observation
X_1, X_2	the first observation, second observation, etc.
Z_i	the i^{th} mean used as an observation
$Y. = \sum_i Y_i$	the sum of the observations $Y_1 + Y_2 + Y_3 + \ldots + Y_n = Y.$
Y_{ijk}	the k^{th} observation in the i^{th} and j^{th} classification. Example: the k^{th} progeny of the i^{th} sire mated to the j^{th} dam.
$\frac{1}{n} \sum_i Y_i = \frac{Y.}{n} = \bar{y}.$	the sample mean of n observations
var	variance
cov	covariance
d.f.	degrees of freedom
SS	sum of squares
SCP	sum of cross products
MS	mean squares
MCP	mean cross products
EMS	expected mean squares
EMCP	expected mean cross products
$<$	is less than
$>$	is greater than
$\geq$	is greater than or equal to

II. Genetic symbols

These symbols are similar to those used in Falconer (1960).

Symbol		Meaning
V_G		genotypic variance where $V_G = V_A + V_D + V_I$
V_A		additive genetic variance
V_D		dominance variance
V_I		interaction variance
	V_{AA}	additive x additive
	V_{AD}	additive x dominance
	V_{DD}	dominance x dominance
	V_{AAA}	additive x additive x additive
	etc.	
V_E		environmental variance
	V_{ES}	special environmental variance (developmental)
	V_{EG}	general environmental variance (microenvironmental
V_M		maternal effects variance
V_C		variance of effects common to families other than maternal, i.e., cage, pen effects or plot effects
V_L		sex linkage
V_{GE}		genotype x environment interaction
V_P		phenotypic variation
r_G		genetic correlation
r_P		phenotypic correlation
r_E		environmental correlation
R		repeatability

Symbol	Meaning
$cov_A(X_1X_2)$	additive genetic covariance between traits X_1 and X_2
$cov_D(X_1X_2)$	dominance covariance between traits X_1 and X_2
$cov_E(X_1X_2)$	environmental covariance between traits X_1 and X_2
$cov_P(X_1X_2)$	phenotypic covariance between traits X_1 and X_2

GENERAL ASSUMPTIONS

In most of the procedures it will be assumed that the base reference population has an inbreeding coefficient of zero. When inbred lines are crossed and the covariances of the relatives determined, the estimates of the genetic variances refer back to this base generation from which the inbred lines were derived. Other assumptions include:

1. There is no linkage except sex linkages.
2. No interference with segregation and independent assortment, i.e., only mendelian inheritance is acting.
3. Regular diploid inheritance.
4. No selection during the formation of inbred lines (Model II assumptions only).

These points are more extensively developed for self-fertilizing species and for estimating genetic variances within an inbred line by Cockerham (1963).

When determining the genetic meaning of a term, the usual method throughout the manual is to use the general formula for the covariance of relatives (Cockerham, 1963)

$$\text{cov} = \alpha V_A + \delta V_D + \alpha^2 V_{AA} + \alpha\delta V_{AD} + \delta^2 V_{DD} + \alpha^3 V_{AAA} + \dots \text{etc.}$$

for half and full sibs. The α and δ are specified in each design. The variance components obtained in the statistical analysis are defined in terms of the covariance of relatives. Solving the general formula gives the genetic meaning of the variance component.

REPEATABILITY

When repeated measurements are made on the same trait of an individual it is possible to calculate the repeatability, R.

I. Equal numbers of measurements per individual

A. Statistical Model

$$Y_{km} = \mu + \alpha_k + e_{km}$$

where Y_{km} is the m^{th} measurement on the k^{th} individual.

Analysis of Variance Table

Source	d.f.	SS	MS	EMS
Between individuals	N-1	SS_W	MS_W	$\sigma_e^2 + k_1\sigma_W^2$
Within individuals between measurements	N (M-1)	SS_e	MS_e	σ_e^2

N = number of individuals
M = number of measurements per individual; equal number for each individual
$k_1 = M$

B. Genetic Model

Source	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{EG}	V_{ES}
σ_W^2	1	1	1	1	1	1	0
σ_e^2	0	0	0	0	0	0	1

The variance component, σ_W^2, has a value because of differences among individuals while σ_e^2 represents the differences among measurements within the individuals. The component σ_W^2 estimates all the genetic variance and the portion of the environmental variance peculiar to the individual.

C. Computations

Analysis of Variance

Source	d.f.	Sum of Squares
Correction term (C.T.)	1	$\frac{Y_{..}^2}{m.}$
Individuals	N - 1	$\sum_k \frac{Y_{k.}^2}{m_k}$ - C.T.
Measurements	N (M - 1)	$\sum\sum_{km} Y_{km}^2 - \sum_k \frac{Y_{k.}^2}{m_k}$

where m_k is the number of measurements on the k^{th} individual

Estimating σ_e^2, σ_W^2 and R

$$\sigma_e^2 = MS_e$$

$$\sigma_W^2 = \frac{MS_W - MS_e}{k_1}$$

$$R = \frac{\sigma_W^2}{\sigma_W^2 + \sigma_e^2} = \text{Repeatability}$$

D. Example: Six turkey females were killed and ten tenderness measurements on the breast muscle per bird were taken. Determine the repeatability of muscle tenderness.

	Female Birds					
	1	2	3	4	5	6
	2.3	2.2	2.1	2.3	2.1	2.0
	2.2	3.1	2.6	2.4	2.0	1.9
	2.2	2.7	2.7	2.1	2.2	2.6
	3.0	2.2	2.0	2.6	2.0	2.5
	2.4	2.5	1.9	2.0	2.0	2.3
	2.8	2.6	1.9	1.7	1.8	2.0
	2.6	2.9	1.8	2.4	2.0	2.5
	2.5	2.3	2.3	2.1	1.7	2.2
	2.2	2.2	2.1	2.5	1.8	2.0
	2.3	3.0	2.2	2.7	1.7	1.7
$Y_{k.}$	24.5	25.7	21.6	22.8	19.3	21.7

$Y_{..} = 135.6$ $Y_{..}^2 = 313.52$

Analysis of Variance

Source	d.f.	SS	MS
Correction term	1	$\frac{(135.6)^2}{60} = 306.45$	---
Individuals	5	$\frac{(24.5)^2 + \ldots + (21.7)^2}{10} = 309.05$ $309.05 - 306.45 = 2.60$	0.520
Measurements	54	$313.52 - 309.05 = 4.47$	0.082

$$\sigma_W^2 = \frac{0.520 - 0.082}{10} = 0.0438$$

$$R = \frac{0.0438}{0.0438 + 0.082} = 0.348$$

II. Unequal numbers of measurements per individual.

In the analysis of variance, divide each $Y_{k.}^2$ by m_k or the number of measurements taken on the k^th individual.

The degrees of freedom for MS_e are the total number of measurements minus the number of individuals.

The coefficient k_1 is $$k_1 = \frac{1}{N-1}\left(m. - \frac{\Sigma m_k^2}{m.}\right)$$

m. = total number of measurements.

III. Standard error and confidence limits

A. Approximate method for standard error. Normality of repeatability and unequal numbers per group is assumed (Swiger, et al., 1964).

$$\text{S.E. } (R) \cong \sqrt{\frac{2(m.-1)\ (1-R)^2\ [1 + (k_1-1)R]^2}{k_1^2(m.-N)(N-1)}}$$

with equal numbers per group then the quantity under the square root sign is multiplied by $\frac{m.\ -\ 1}{m.}$

In the example R = 0.348. The S.E. (equal nos.) is

$$\text{S.E. } (R) \cong \sqrt{\frac{2(60-1)(1-0.348)^2\ [1 + (10-1)0.348]^2}{10^2(60-6)(6-1)}\left(\frac{60-1}{60}\right)}$$

$$\cong \sqrt{(0.03171)(0.983)} = \sqrt{0.03117}$$

$$\cong 0.177$$

$$R = 0.348 \pm 0.177$$

B. Confidence limits for repeatability (Bogyo and Becker, 1963). Normality of repeatability does not have to be assumed.

The confidence statement is

$$P[1-K_{\alpha/2} \leq R \leq 1-K_{1-\alpha/2}] = 1 - \alpha$$

$$\text{where } K_r = \frac{k_1 MS_e Fr}{MS_w + MS_e(k_1-1)F_r}$$

F_r = tabled values of F distribution

$1-\alpha$ = level of confidence

In the examples, the 0.95 confidence limits ($\alpha = 0.05$) would be obtained as follows:

The value for $F_{.025(5,54)}$ is given in the F tables for 5 d.f. in the numerator and 40 d.f. in the denominator.

$$F_{.025} = 2.90$$

The value for $F_{.975}$ is obtained by reversing the degrees of freedom and taking reciprocal of tabled value. Use 40 d.f. for numerator and 5 d.f. for denominator and take reciprocal.

$$F_{.975} = \frac{1}{6.18} = 0.162$$

Then

$$K_{.025} = \frac{10(0.082)(2.90)}{0.520 + 0.082(10-1)(2.90)} = 0.8939$$

$$K_{.975} = \frac{10(0.082)(0.162)}{0.520 + 0.082(10-1)(0.162)} = 0.2076$$

$$P\,[1-0.894 \le 0.348 \le 1-0.208] = 0.95$$

$$P\,[0.106 \le 0.348 \le 0.792] = 0.95$$

IV. Uses of repeatability

A. Multiple records

Heritability is usually given in terms of one record per individual. When there is more than one record then the heritability is larger. The factor by which the heritability is multiplied is given in table 1 for up to six records.

B. Upper estimate of heritability

The genetic model shows that σ^2_W estimates all the genetic variance plus a portion of the environmental variance. Thus R would be an overestimate of heritability.

ESTIMATION OF VARIANCE COMPONENTS AND HERITABILITY

Variance components from the analysis of variance computations provide estimates of various genetic parameters. The design is usually determined by the reproductive requirements of the species.

I. One-way layout

A. Equal numbers of progeny per sire group

This design is useful for uniparous animals with a long generation interval such as cattle. Each sire is mated to several dams and each dam produces one progeny. The measurement is taken on the progeny. The reference population is the population from which the sires and dams were obtained.

1. Models

a. Statistical

Random Model II

$$Y_{ik} = \mu + \alpha_i + e_{ik}$$

where Y_{ik} is the observation on the k^{th} individual from the i^{th} sire.

Analysis of Variance Table

Source of variation	d.f.	SS	MS	EMS
Between sires	S-1	SS_S	MS_S	$\sigma_W^2 + k\sigma_S^2$
Progeny within sires	n. - S	SS_W	MS_W	σ_W^2

S = number of sires

n_i = number of individuals within the i^{th} sire = number of dams mated to the i^{th} sire

k = n_i in expected mean squares

n. = total number of individuals

b. Genetic

The size of the variance component σ_S^2 is due to the fact that the sire groups differ. These groups are made up of half sibs, and therefore, the variance component σ_S^2 is equivalent to the covariance among half sibs.

The general formula is:

$$cov = \alpha V_A + \delta V_D + \alpha^2 V_{AA} + \delta^2 V_{DD} + \alpha\delta V_{AD} + \alpha^3 V_{AA} + \ldots\ldots\ldots \text{ etc.}$$

The coefficients α and δ for covariance of half sibs are:

	α	δ
cov_{HS}	1/4	0

Substituting the coefficients in the formula

$$cov_{HS} = 1/4V_A + 1/16V_{AA} + 1/64\ V_{AA} + \ldots\ldots\ldots$$

The variance component σ_W^2 has the meaning $\sigma_T^2 - cov_{HS}$ where σ_T^2 is the total variance.

The two components estimate the following:

Component	Covariance								Heterogametic Males		Heterogametic Females	
									♂♂	♀♀	♂♂	♀♀
		V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_E	V_L	V_L	V_L	V_L
σ_S^2	cov_{HS}	1/4	0	1/16	0	0	1/64	0	0	1/2	1/4	1/2
σ_W^2	$\sigma_T^2 - cov_{HS}$	3/4	1	15/16	1	1	63/64	1	1	1/2	3/4	1/2

The variance component σ_S^2 estimates 1/4 of the additive genetic variance, 1/16 of the additive x additive genetic variance and various amounts of the sex linkage variance depending upon the sex and species. The variance component σ_W^2 estimates the remainder of the genetic variance plus all the environmental variance.

2. Computation formulas

Source of variation	Sum of squares	Mean square
Correction Term (C.T.)	$\frac{Y^2_{..}}{n.}$	--
Between sires	$\Sigma_i \frac{Y^2_{i.}}{n_i} - \text{C.T.}$	$SS_S/S-1$
Progeny within sires	$\Sigma_i \Sigma_k Y^2_{ik} - \Sigma \frac{Y^2_{i.}}{n_i}$	$SS_W/n.-S$

Estimating σ^2_S and h^2_S,

$$\sigma^2_S = \frac{MS_S - MS_W}{k},$$

$$h^2_S = \frac{4\ \sigma^2_S}{\sigma^2_S + \sigma^2_W}$$

3. Example:

Five chicken sires were mated to eight dams each and each mating produced one progeny per dam or eight progeny per sire. Eight-week body weights in grams were as follows:

	Sires				
	A	B	C	D	E
	687	618	618	600	717
	691	680	687	657	658
	793	592	763	669	674
	675	683	747	606	611
	700	631	678	718	678
	753	691	737	693	788
	704	694	731	669	650
	717	732	603	648	690
$Y_{i.}$	5720	5321	5564	5260	5466

$Y_{..} = 27{,}331$ $\quad \underset{ik}{\Sigma\Sigma}\, Y^2_{ik} = 18{,}773{,}473$ $\quad n. = 40$ $\quad n_i = k = 8$

Correction term $\frac{(27{,}331)^2}{40} = 18{,}674{,}589$

Between sires $\frac{(5720)^2}{8} + \frac{(5321)^2}{8} + \frac{(5564)^2}{8} + \frac{(5466)^2}{8} = 18{,}691{,}786$

With equal numbers of progeny/sire it is easier to calculate the between sires uncorrected sum of squares as follows:

$$\frac{(5720)^2 + (5321)^2 + (5564)^2 + (5260)^2 + (5466)^2}{8}$$

With unequal numbers per sire, each term has to be calculated separately because the denominators will differ from family to family.

$$SS_S = 18,691,786 - 18,674,589 = 17,197$$

$$SS_W = 18,773,473 - 18,691,786 = 81,687$$

Analysis of Variance Table

	d.f.	S.S.	Mean Square
Between sires	(5-1)=4	17,197	4,299
Progeny within sires	(40-5)=35	81,687	2,334

$$\sigma^2_S = \frac{4,299 - 2,334}{8} = 246$$

$$h^2_S = \frac{(4)\ 246}{246 + 2,334} = 4 \times 0.095 = 0.38$$

B. Unequal numbers of progeny per sire

1. Coefficient, k.

The analysis of variance is computed as above except that the coefficient k has to be calculated by the formula

$$k = \frac{1}{S-1} \quad (n. - \frac{\Sigma n_i^2}{n.})$$

Example: Five sires were each mated to eight dams but not all dams produced a progeny.

Sire	No. Progeny
A	8
B	4
C	5
D	6
E	8

The coefficient, k, is

$$k = \frac{1}{4} \quad (31 - \frac{8^2 + 4^2 + 5^2 + 6^2 + 8^2}{31}) = 6.10$$

2. Standard error and confidence limits to heritability

a. Approximate method for standard error. (Swiger et al., 1964) Normality of the intraclass correlation, t, is assumed.

$$\text{S. E. } (h_S^2) = 4\sqrt{\frac{2(n.-1)\ (1-t)^2\ [1 + (k-1)t]^2}{k^2\ (n.-S)\ (S-1)}}$$

where t is the intra-class correlation

$$t = \frac{\sigma_S^2}{\sigma_S^2 + \sigma_W^2}$$

This method also applies to equal numbers per sire in which case the quantity under the square root sign is multiplied by $\frac{n.-1}{n.}$

In the example

$$t = \frac{246}{246 + 2{,}334} = 0.095$$

$$\text{S. E. } (h_S^2) = 4\sqrt{\frac{2\ (40-1)\ (1-0.095)^2\ [1 + (8-1)\ 0.095]^2}{8^2\ (40-5)\ (5-1)}}$$

$$= 4\sqrt{0.01976} = 0.562$$

This would be the solution if the example had unequal numbers. With equal numbers it is

$$4\sqrt{(0.01976)\ \frac{(40-1)}{40}} = 4\sqrt{0.01927}$$

$$= 4\ (0.139)$$

$$= 0.556$$

So $h_S^2 = 6.38 \pm 0.56$

Thus, with equal numbers the standard error will be lower than with unequal numbers per sire.

3. Confidence limits on heritability estimate

An exact method for determining confidence limits when there are equal numbers per sire is given by Bogyo and Becker (1963). This method is approximate when there are unequal numbers and the coefficient, k, is used. Normality of the interclass correlation is not required.

The confidence statement is

$$P\ [4\ (1-K_{\alpha/2}) \leq h^2 \leq 4\ (1-K_{1-\alpha/2}) = 1 - \alpha$$

where

$$K_r = \frac{k\ MS_W\ F_r}{MS_S + MS_W\ (k-1)\ F_r}$$

F_r = tabled values of the F distribution

$1 - \alpha$ = level of confidence

In the example, the .95 confidence limits ($\alpha = 0.05$) would be obtained as follows:

The nearest value for $F_{.025}\ (4,35)$ in the usual tables is given for 4 d.f. in the numerator and 30 d.f. in the denominator. Therefore,

$$F_{.025} = 3.25$$

The value for $F_{.975}$ is obtained by reversing the degrees of freedom and taking the reciprocal of the tabled value. Using 30 d.f. for the numerator d.f. because 35 d.f. is not given and 4 d.f. for the denominator d.f. and taking the reciprocal

$$F_{.975} = \frac{1}{8.46} = 0.118$$

Then

$$K_{.025} = \frac{8\ (2,334)\ (3.25)}{4,299 + 2,334\ (8-1)(3.25)} = 1.05735$$

$$K_{.975} = \frac{8\ (2,334)\ (0.118)}{4,299 + 2,334\ (8-1)(0.118)} = 0.3538$$

$$P\ [4(1-1.573) \leq 0.38 \leq 4(1-0.3538)] = 0.95$$

$$P\ [-0.229 \leq 0.38 \leq 2.58] = 0.95$$

The standard error is large and the confidence limits are wide because of the small number of sires used in this example.

C. Single pair matings

This design can be utilized with multiparous animals such as mice, rats or swine, and also animals that produce large amounts of eggs in a short time (Coturnix quail, chickens, turkeys, Drosophila and Tribolium). Plants can be mated to fit this design.

Pairs of individuals are chosen at random from the reference population and mated together. Each mating produces several offspring.

1. Models

a. Statistical

Random Model II

$$Y_{ik} = u + \alpha_i + e_{ik}$$

where Y_{ik} is the observation on the k^{th} individual from the i^{th} mating.

Analysis of Variance Table

Source of variation	d.f.	SS	MS	EMS
Between matings	S-1	SS_S	MS_S	$\sigma^2_W + k\,\sigma^2_S$
Progeny within matings	n.-S	SS_W	MS_W	σ^2_W

S = number of matings
n_i = number of individuals within the i^{th} mating
k = n_i in expected mean squares
n. = total number of individuals

b. Genetic

The variance component, σ^2_S, is due to the fact that the mating groups differ. The members of these groups are composed of full sibs and therefore the component is equivalent to covariance of full sibs. The coefficients α and δ for covariance of full sibs are:

	α	δ
cov_{FS}	2/4	1/4

Substituting the coefficients in the general formula

$$cov_{FS} = 2/4V_A + 1/4V_D + 1/4V_{AA} + 1/16\ V_{DD} + 2/16V_{AD} + 2/16V_{AAA} + \ldots\ldots\ \text{etc.}$$

The component σ^2_W has the meaning $\sigma^2_T - cov_{FS}$.

The two components estimate

Component	Covariance	V_A	V_D	V_{AA}	V_{DD}	V_{AD}	V_{AAA}	V_M	V_E
σ_S^2	cov_{FS}	2/4	1/4	1/4	1/16	2/16	2/16	1	0
σ_W^2	$\sigma_T^2 - cov_{FS}$	2/4	3/4	3/4	15/16	4/16	4/16	0	1

The variance component σ_S^2 estimates 1/2 of the additive genetic variance, 1/4 of the dominance variance and various amounts of the epistatic variance.

The component σ_W^2 estimates the remainder of the genetic variance plus the environmental variance.

2. Computation formulas

The analysis of variance formulas are the same as on page 8 for both equal and unequal numbers of progeny per mating.

The heritability is $h^2 = \dfrac{2\,\sigma_S^2}{\sigma_S^2 + \sigma_W^2}$

The numerator contains an estimate of 1/2 the dominance variance and all the maternal effects variance. If the dominance and maternal effects variance equals zero then this heritability will be the same as the previous heritability except for additive interactions.

The standard error is

$$S.E.\ (h^2) = 2\sqrt{\frac{2(n.-1)(1-t)^2\ [1 + (k-1)\ t]^2}{k^2(n.-S)(S-1)}}$$

for unequal numbers. With equal numbers multiply quantity under the square root sign by $\frac{n.-1}{n.}$.

The confidence limits are

$$P\ [2(1-K_{\alpha/2}) \leq h^2 \leq 2(1-K_{1-\alpha/2})] = 1-\alpha$$

II. Nested or hierarchal design

In this design each sire (paternal plant) is mated with several dams (maternal plants) and each mating produces several progeny.

The reference population is a non-inbred random mating population. Non-related animals or plants can be taken at random from the population and mated (inbreeding coefficient $F = 0$). Inbred lines can be formed from this population with no selection among or within the lines. The lines are crossed (paternal lines x maternal lines) and the estimates of parameters refer to the base non-inbred population.

A. Animals

The design given here assumes that the individuals are chosen at random from the reference population and that the inbreeding coefficient is zero.

1. Statistical model

$$Y_{ijk} = \mu + \alpha_i + \beta_{ij} + e_{ijk}$$

where Y_{ijk} is the record of the k^{th} progeny of the j^{th} dam mated to the i^{th} sire; μ is the common mean; α_i = effect of the i^{th} sire; β_{ij} is the effect of the j^{th} dam mated to the i^{th} sire and e_{ijk} = the uncontrolled environmental and genetic deviations attributable to the individuals.

Analysis of Variance Table

Source of variation	d.f.	SS	MS	EMS
Between sires	S-1	SS_S	MS_S	$\sigma_W^2 + k_2\sigma_D^2 + k_3\sigma_S^2$
Between dams within sires	D-S	SS_D	MS_D	$\sigma_W^2 + k_1\sigma_D^2$
Progeny within dams	n..-D	SS_W	MS_W	σ_W^2

S = number of sires
D = total number of dams
n.. = total number of progeny

With equal numbers of dams/sire and progeny/dam
$k_1 = k_2$ = number of progeny per dam
k_3 = number of progeny per sire

With unequal numbers of dams per sire and unequal numbers of progeny per dam the coefficients k_1, k_2, and k_3 have to be computed differently.

2. Genetic model

The component, σ^2_S, is due to the sire groups being different. These groups consist of half sibs so σ^2_s is the covariance of half sibs.

The component σ^2_D is derived from the differences between dam groups. These groups are composed of full sibs so that σ^2_D is the covariance of full sibs minus the covariance of sires half sib groups because the sire effect is removed in the analysis of variance. Thus, $\sigma^2_D = cov_{FS} - cov_{HS}$.

The coefficients α and δ are:

	α	δ
cov_{HS}	1/4	0
cov_{FS}	2/4	1/4

The covariance of half sibs estimates

$$cov_{HS} = 1/4V_A + 1/16V_{AA} + 1/64V_{AA} + \dots\dots\dots$$

The covariance of full sibs estimates

$$cov_{FS} = 2/4V_A + 1/4V_D + 1/4V_{AA} + 1/8V_{AD} + 1/16V_{DD} + 1/8V_{AAA} + \dots\dots$$

The component σ^2_W contains the remainder of the genetic variance and the environmental variance.

The genetic and environmental interpretation of the components is given in the table (F = 0).

										Heterogametic			
										Males		Females	
										♂♂	♀♀	♂♂	♀♀
Components	Covariances	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E	V_L	V_L	V_L	V_L
σ^2_S	cov_{HS}	$\frac{1}{4}$	0	$\frac{1}{16}$	0	0	$\frac{1}{64}$	0	0	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$
σ^2_D	$cov_{FS} - cov_{HS}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{7}{64}$	1	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	0
σ^2_W	$\sigma^2_T - cov_{FS}$	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{7}{8}$	$\frac{15}{16}$	$\frac{7}{8}$	0	1	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$
$\sigma^2_S + \sigma^2_D$	cov_{FS}	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{8}$	1	0	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{1}{2}$

Note that σ^2_D contains all the maternal effects variance, V_M, an important element of traits measured early in the life of animals.

3. Computational formulas

Source of variation	Sum of squares	Mean square
Correction term (C.T.)	$\dfrac{Y^2_{\cdots}}{n_{\cdot\cdot}}$	
Between sires	$\sum_i \dfrac{Y^2_{i\cdot\cdot}}{n_{i\cdot}} - \text{C.T.}$	$SS_S \big/ S-1$
Between dams	$\sum_i \sum_j \dfrac{Y^2_{ij\cdot}}{n_{ij}} - \sum_i \dfrac{Y^2_{i\cdot\cdot}}{n_{i\cdot}}$	$SS_D \big/ D-S$
Progeny within dams	$\sum_i \sum_j \sum_k Y^2_{ijk} - \sum_i \sum_j \dfrac{Y^2_{ij\cdot}}{n_{ij}}$	$SS_W \big/ n_{\cdot\cdot}-D$

Estimating variance components:

$$\sigma^2_W = MS_W$$

$$\sigma^2_D = \frac{MS_D - MS_W}{k_1}$$

$$\sigma^2_S = \frac{MS_S - (MS_W + k_2\sigma^2_D)}{k_3}$$

With equal numbers, $k_1 = k_2$ and

$$\sigma^2_S = \frac{MS_S - MS_D}{k_3}$$

With unequal numbers the coefficients are calculated as follows:

$$k_1 = \frac{n_{\cdot\cdot} - \sum_i \dfrac{\sum_j n^2_{ij}}{n_{i\cdot}}}{\text{D-S or d.f. for dams}}$$

$$k_2 = \frac{\dfrac{\sum_i \sum_j n^2_{ij}}{n_{i\cdot}} - \dfrac{\sum_i \sum_j n^2_{ij}}{n_{\cdot\cdot}}}{\text{S-1 or d.f. for sires}}$$

$$k_3 = \frac{n_{..} - \dfrac{\sum_i n_{i.}^2}{n_{..}}}{S-1}$$

Standard errors of components

The general formula is (Anderson and Bancroft, 1952)

$$\text{S. E.} \cong \sqrt{\frac{2}{k^2} \sum_g \frac{MS_g^2}{f_g + 2}} = \sqrt{\text{var } (\sigma_g^2)}$$

where k = coefficient of the variance component being estimated, MS_g = the g^{th} mean square used to estimate the variance component, and f_g = the degrees of freedom of the g^{th} mean square.

$$\text{S.E. } (\sigma_S^2) \cong \sqrt{\frac{2}{k_3^2} \left(\frac{MS_S^2}{S + 1} + \frac{MS_D^2}{D-S+2} \right)}$$

Heritabilities

$$h_S^2 = \frac{4 \sigma_S^2}{\sigma_S^2 + \sigma_D^2 + \sigma_W^2}$$

$$h_D^2 = \frac{4 \sigma_D^2}{\sigma_S^2 + \sigma_D^2 + \sigma_W^2}$$

This estimate of heritability contains four times the maternal effects and all dominance variance in its numerator.

$$h_{S + D}^2 = \frac{2(\sigma_S^2 + \sigma_D^2)}{\sigma_S^2 + \sigma_D^2 + \sigma_W^2}$$

This estimate, based upon full sibs, contains two times the maternal effects and one-half the dominance variance.

Standard errors of heritabilities (modified from Dickerson, 1960)

$$\text{S.E. } (h_S^2) \cong \frac{4\sqrt{\text{var}(\sigma_S^2)}}{\sigma_S^2 + \sigma_D^2 + \sigma_W^2}$$

$$\text{S.E. } (h_D^2) \cong \frac{4\sqrt{\text{var}(\sigma_D^2)}}{\sigma_S^2 + \sigma_D^2 + \sigma_W^2}$$

$$\text{S.E. } (h_{S+D}^2) \cong \frac{2\sqrt{\text{var}(\sigma_S^2) + \text{var}(\sigma_D^2) + 2\ \text{cov}(\sigma_S^2\ \sigma_D^2)}}{\sigma_S^2 + \sigma_D^2 + \sigma_W^2}$$

where $\text{cov}\ (\sigma_S^2\ \sigma_D^2) = -\ \frac{k_2}{k_3}\left(\text{var}\ (\sigma_D^2) - \frac{2\ MS_W^2}{k_1^2\ (n..-D+2)}\right)$

4. Example. From a large non-inbred population of White Rock chickens, five sires and fifteen dams were chosen at random and mated, one sire to three dams. Each dam produced three female progeny. The 8-week body weights of these progeny were recorded to the nearest gram. What are the estimates of heritability for this population?

Sires	Dams	Progeny weight			$Y_{ij.}$	$Y_{i..}$
A	1	965	813	765	2543	
	2	803	640	714	2157	
	3	644	753	705	2102	6802
B	4	740	798	941	2479	
	5	701	847	909	2457	
	6	909	800	853	2562	7498
C	7	696	807	800	2303	
	8	752	863	739	2354	
	9	686	832	796	2314	6971
D	10	979	798	788	2565	
	11	905	880	770	2555	
	12	797	721	765	2283	7403
E	13	809	756	775	2340	
	14	887	935	937	2759	
	15	872	811	925	2608	7707

$Y_{...} = 36,381$

$$\sum_i \sum_j \sum_k Y_{ijk}^2 = 29,729,879$$

$n_{..}$ = total number of progeny = 45

$n_{i.}$ = number of progeny per sire = 9

n_{ij} = number of progeny per dam = 3

S = number of sires = 5

D = number of dams = 15

Analysis of Variance

Source of Variation

Correction term (C.T.) $\frac{(36,381)^2}{45} = 29,412,825$

Between Sires $\frac{(6802)^2 + (7498)^2 + (6971)^2 + (7403)^2 + (7707)^2}{9} = 29,476,034$

With unequal numbers each squared sum would be divided by the number of progeny within the group.

$SS_S = 29,476,034 - 29,412,825 = 63,209$

Between Dams $\frac{(2543)^2 + (2157)^2 + \ldots + (2608)^2}{3} = 29,564,147$

$SS_D = 29,564,147 - 29,476,034 = 88,113$

Progeny within dams, $SS_W = 29,729,879 - 29,564,147 = 165,732$

Source	d.f.	Sum of Squares	Mean Squares
Sires	(5 - 1) = 4	63,209	15,802
Dams	(15 - 5) = 10	88,113	8,811
Progeny	(45 -15) = 30	165,632	5,524

$\sigma^2_W = 5,524$

$\sigma^2_D = \frac{8,811-5,524}{3} = 1,095$

$$\text{S.E. } (\sigma^2_D) = \sqrt{\frac{2}{3^2}\left[\frac{(8,811)^2}{10 + 2} + \frac{(5,524)^2}{30 + 2}\right]} = 1,284$$

$\sigma^2_S = \frac{15,802 - 8,811}{9} = 776$

$$\text{S.E. } (\sigma^2_S) = \sqrt{\frac{2}{9^2}\left[\frac{(15,802)^2}{4 + 2} + \frac{(8,811)^2}{10 + 2}\right]} = 1,090$$

Estimating heritability

$$h^2_S = \frac{4(776)}{776 + 1{,}095 + 5{,}524} = \frac{3{,}104}{7{,}395} = 0.42$$

$$\text{S.E. } (h^2_S) = \frac{4(1{,}090)}{7{,}395} = 0.58$$

$$h^2_D = \frac{4(1{,}095)}{7{,}395} = 0.59$$

$$\text{S.E. } (h^2_D) = \frac{4(1{,}284)}{7{,}395} = 0.69$$

This estimate of heritability is larger than h^2_S possibly because of maternal effects.

$$h^2_{(S + D)} = \frac{2(776 + 1{,}095)}{7{,}395} = 0.51$$

$$\text{S.E. } (h^2_{S + D}) = \frac{2\sqrt{1{,}188{,}100 + 1{,}648{,}656 - 478{,}916}}{7{,}395} = 0.49$$

$$\text{where cov } (\sigma^2_S, \sigma^2_D) = -\frac{3}{9}\left[1{,}648{,}656 - \frac{2\ (5{,}524)^2}{3^2\ (45 - 15 + 2)}\right]$$

This heritability estimate contains lesser amounts of maternal effects and dominance variance than h^2_D.

The standard errors are high because of the small numbers of sires and dams used in this example.

Unequal numbers

With unequal numbers of dams per sire and progeny per dam the coefficients have to be determined by previously given formulas.

Example. Each of five sires were mated to differing numbers of dams and the dams produced unequal numbers of female progeny.

Number	Sires				
	A	B	C	D	E
Of dams	3	5	4	2	5
Of progeny per dam (n_{ij})	5,4,6	4,10, 6,7,9	7,5, 4,1	8,6	1,5,3, 6,4
Of progeny per sire ($n_{i.}$)	15	36	17	14	19

$n_{..} = 101$

$$k_1 = \frac{101 - \left(\frac{5^2 + 4^2 + 6^2}{15} + \frac{4^2 + 10^2 + 6^2 + 7^2 + 9^2}{36} + \frac{7^2 + 5^2 + 4^2 + 1^2}{17}\right.}{14}$$

$$\frac{+ \frac{8^2 + 6^2}{14} + \left.\frac{1^2 + 5^2 + 3^2 + 6^2 + 4^2}{19}\right)}{14} = \frac{101 - 30.04}{14} = 5.07$$

$$k_2 = \frac{30.04 - \frac{5^2 + 4^2 + 6^2 + 4^2 + 10^2 + \ . \ . \ . + 4^2}{101}}{4} = \frac{30.04 - \frac{637}{101}}{4} = 5.933$$

$$k_3 = \frac{101 - \frac{15^2 + 36^2 + 17^2 + 14^2 + 19^2}{101}}{4} = \frac{101 - 23.435}{4} = 19.391$$

σ^2_W and σ^2_D are estimated as before but because $k_1 \neq k_2$ the estimate of σ^2_S is obtained as follows:

$$\sigma^2_S = \frac{MS_S - MS_W - \frac{k_2}{k_1}(MS_D - MS_W)}{k_3}$$

The calculations for heritabilities and their standard errors are the same as before.

Other effects such as years, hatches or farms may be superimposed upon the preceding model. Refer to King and Henderson (1954) for a worked example.

B. Plants

The mating design is as before with animals except that the full sib progeny are planted in plots within blocks (replicates). Comstock and Robinson (1952) present this design as Experiment I. The replicates are considered fixed and there is only one plot per mating within a replicate. Crosses among inbred lines are also included in this design.

1. Statistical model

The formula is:

$$Z_{hij} = \mu + \alpha_i + \beta_{ij} + \delta_h + e_{hij}$$

where Z_{hij} is the plot mean within the h^{th} replicate of the i^{th} paternal plant (or inbred line) and the j^{th} maternal plant (or inbred line). μ is common to all observations, α_i is the effect of the i^{th} paternal plant (line), β_{ij} is the effect of the j^{th} maternal plant (line) mated to the i^{th} paternal plant (line), δ_h is the effect of the h^{th} replication, and e_{hij} is the environmental and remainder of genetic variance among plots.

Missing plots can be estimated by the method described by Snedecor (1956 pp. 310).

Analysis of Variance of Plot Means - 1

Source of Variation	d.f.	SS	MS	EMS
Replicates	R-1	SS_R	MS_R	
Paternal plants	S-1	SS_S	MS_S	$\sigma_c^2 + n_k\sigma_W^2 + k_2\sigma_D^2 + k_3\sigma_S^2$
Maternal within paternal plots	S(d-1)	SS_D	MS_D	$\sigma_c^2 + n_k\sigma_W^2 + k_1\sigma_D^2$
Paternal-maternal crosses x replicate	(Sd-1)(R-1)	SS_I	MS_I	$\sigma_c^2 + n_k\sigma_W^2$

R = number of replicates
S = number of paternal plants (lines)
d = number maternal plants (lines) per paternal plant (line)
$k_1 = k_2$ = number of plots per maternal plant (line)
k_3 = number of plots per paternal plant (line)

$$n_k = \frac{1}{RSd} \sum_h \sum_i \sum_j \frac{1}{n_{hij}} = \text{reciprocal of the harmonic mean of the individuals per plot}$$

where n_{hij} = the number of full sibs in the h^{th} replicate from the i^{th} paternal plant (line) crossed with the j^{th} maternal plant (line).

Because of unequal numbers of progeny per plot an estimate of the individual variance within plots is obtained using the individual observations.

The formula is:

$$Y_{fk} = \mu + P_f + e_{fk}$$

where Y_{fk} = the individual observation on the k^{th} individual of the f^{th} plot, μ is the grand mean, P is the effect of the f^{th} plot and e_{fk} is the environmental and genetic variance among full sibs within plots.

Analysis of Variance of Individuals - 2

Source of Variations	d.f.	SS	MS	EMS
Between plots	RSd-1	SS	--	--
Between full sibs within plots	$n_{..}$ - RSd	SS_W	MS_W	σ^2_W

$n_{..}$ = total number of individuals

See Kempthorne (1957, pp. 459)

2. Genetic Model

This model is similar to that given for animals. The variance component, σ^2_S, is due to the half sib groups being different among paternal plants so this component is the covariance of half sibs.

The component, σ^2_D, is obtained from differences between maternal plants so that σ^2_D is covariance of full sibs minus the covariance of half sibs (paternal plant groups). Then

$$\sigma^2_D = \mathrm{cov}_{FS} - \mathrm{cov}_{HS}$$

If single plants are used from a non-inbred base population (F=0) or a single plant represents each inbred line so that there is a set of paternal inbred lines and a set of maternal inbred lines then the coefficients α and δ are:

Covariance	α	δ
cov_{HS}	$\frac{1 + F_S}{4}$	0
cov_{FS}	$\frac{2 + F_S + F_D}{4}$	$\frac{(1 + F_S)(1 + F_D)}{4}$

where F_S = the inbreeding coefficient of the paternal lines, each line having the same inbreeding coefficient and F_D = the inbreeding coefficient of the maternal lines. If the inbreeding differs among lines within a set an average coefficient may be used although this introduces some inaccuracies in the estimation of the genetic variances.

The covariance of half sibs estimates

$$\mathrm{cov}_{HS} = \frac{1 + F_S}{4} V_A + \left(\frac{1 + F_S}{4}\right)^2 V_{AA} + \text{------}$$

The covariance of full sibs estimates

$$\mathrm{cov}_{FS} = \frac{2 + F_S + F_D}{4} V_A + \frac{(1 + F_S)(1 + F_D)}{4} V_D + \left(\frac{2 + F_S + F_D}{4}\right)^2 V_{AA} +$$
$$\left(\frac{2 + F_S + F_D}{4}\right) \frac{(1 + F_S)(1 + F_D)}{4} V_{AD} + \left[\frac{(1 + F_S)(1 + F_D)}{4}\right]^2 V_D +$$
$$\cdots\cdots\cdots$$

The variance components estimate

$$\sigma^2_S = \mathrm{cov}_{HS}$$

$$\sigma^2_D = \mathrm{cov}_{FS} - \mathrm{cov}_{HS}$$

$$\sigma^2_W = \sigma^2_T - \mathrm{cov}_{FS}$$

If bulked pollen from at least six plants is obtained from each paternal line and used to fertilize at least six plants in each maternal line then the analysis can be carried out on the plot means or totals. Plants such as cereals require this type of analysis.

Only analysis of variance of plot means - 1 is used and the source of variation refers to lines rather than plants. The variance component σ^2_S refers to differences between lines with a paternal line in common crossed to maternal lines. Thus, there is no reference to half or full sibs but to one line in common A-, A- and two lines in common AB, AB. (See Cockerham, 1961).

The coefficients for the general formula are:

Covariances	α	δ
$\mathrm{cov}_{A-,\ A-}$	$F/2$	0
$\mathrm{cov}_{AB,\ AB}$	F	F^2

It is assumed throughout that the inbreeding of the maternal and paternal lines are the same.

With F = 1 in both paternal and maternal inbred lines the genetic meaning is:

Components	Covariances	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E
σ^2_S	$cov_{A-,A-}$	1/2	0	1/4	0	0	1/8	0	0
σ^2_D	$cov_{AB,AB}-cov_{A-,A-}$	1/2	1	3/4	1	1	7/8	1	0
σ^2_W	$\sigma^2_T - cov_{AB,AB}$	0	0	0	0	0	0	0	1
$\sigma^2_D + \sigma^2_S$	$cov_{AB,AB}$	1	1	1	1	1	1	1	0

Here the covariance of full sibs estimates all the genetic variance. Note that genetic meaning is the same when single plants are used if F = 1.

3. Computational formulas

The symbol Z designates the plot mean.

Analysis of Variance of Plot Means -2

Source of Variation	Sum of Squares	Mean Squares
Correction term (C.T.)	$\frac{Z^2_{...}}{RSd}$	
Replications	$\sum_h \frac{Z^2_{h..}}{Sd} - C.T.$	$SS_{R/R-1}$
Paternal plants	$\sum_i \frac{Z^2_{.i.}}{Rd} - C.T.$	$SS_{S/S-1}$
Maternal plants within paternal plants	$\sum_j \frac{Z^2_{..j}}{RS} - \sum_i \frac{Z^2_{.i.}}{Rd}$	$SS_{D/S(d-1)}$
Paternal-maternal crosses x replicates	$\sum\sum\sum_{hij} Z^2_{hij} - \sum_j \frac{Z^2_{..j}}{RS} - \sum_h \frac{Z^2_{h..}}{Sd} + C.T.$	$SS_{I/(Sd-1)(R-1)}$

In computing with individual plants Y is the symbol.

Analysis of Variance of Individual Plants -2

Source of Variation	Sum of Squares	Mean Squares
Between plots	$\sum_f \frac{Y^2_{f.}}{n_f} - C.T.$	
Within plots	$\sum\sum_{fk} Y^2_{fk} - \sum_f \frac{Y^2_{f.}}{n_f}$	$SS_W/_{n.. - Rds}$

Estimating variance components

$$\sigma_S^2 = \frac{MS_S - MS_D}{k_3}$$

$$\sigma_D^2 = \frac{MS_D - MS_I}{k_1}$$

$$\sigma_W^2 = MS_W$$

$$\sigma_c^2 = MS_I - n_k \, MS_W$$

Standard error of the components

The general formula is the same as given on page 17.

$$\text{S.E.} \approxeq \sqrt{\frac{2}{k^2} \sum_g \frac{MS_g^2}{f_g + 2}}$$

where k = coefficient of variance component, MS_g = g^{th} mean square, f_g = degrees of freedom of the g^{th} mean square.

Heritabilities

Heritabilities of an individual plant are not too useful because most plants are not selected on the basis of their individual performance. Certain exceptions should be noted e.g. trees. The concept of the heritability of a selection unit (Hanson, 1963) is used as a practical measure. Here the numerator is the additive genetic variance appropriate to the unit and the denominator is the phenotypic variance of the unit. See also Namkoong, et al. (1966); Squillace, et al. (1967).

III. Factorial design

This design can be used with both plants and animals. Each sire (paternal plant) is mated with every dam (maternal plant) and each mating produces several progeny.

The reference population is large, non-inbred, and random-mated. Non-related animals can be taken at random from the population and mated (F = 0).

Inbred lines can be obtained from the reference base population and mated together to obtain estimates of genetic parameters that refer back to the base population.

A. Animals

The main difficulty with animals is that in most species the female cannot be mated to several males simultaneously. Therefore, it is necessary to shift males from one dam to another introducing a time element and some uncertainty concerning the sire of later progeny because of residual fertility. With most marine animals this problem is overcome because the female produces large amounts of non-fertilized eggs that can be apportioned and then fertilized by several sires.

Because a sire can be mated only to a certain number of dams the concept of a "set" will be used. The mating plan for one set of sires and dams is given below. Shifts will be considered random. A number of sets constitute the experiment.

	Dams					
Sires	1	2	3	4	5	6
1	X_I	X_I	X_{II}	X_{II}	X_{III}	X_{III}
2	X_{II}	X_{II}	X_{III}	X_{III}	X_I	X_I
3	X_{III}	X_{III}	X_I	X_I	X_{II}	X_{II}

Thus sire 1 is mated to dams 1 and 2 in shift I, to dams 3 and 4 in shift II and to dams 5 and 6 in shift III. The above pattern constitutes a set. It is also possible to use two sires per set reducing the number of shifts and decreasing the time element.

It will be assumed that there are no zero subclasses, i.e. all matings produce measureable progeny, that each set has the same number of sires and dams as every other set and that there are unequal numbers of full sib progeny per mating.

Two analyses will be made. One analysis uses the mean of the full sib progeny of each subclass and the other analysis obtains the full sib variation using the individual progeny's records.

1. Statistical model

The formula for this model incorporating both analyses is

$$Y_{ijklm} = \mu + \alpha_{il} + \beta_{jl} + \delta_{lm} + Y_{l} + (\alpha\beta)_{ijl} + (\alpha\delta)_{ilm} + (\beta\delta)_{jlm} + e_{ijklm}$$

where Y_{ijklm} is the observation on the k^{th} individual from a mating of the i^{th} sire with the j^{th} dam in the m^{th} shift in the l^{th} set. μ is the common mean; α_{il} is the effect of the i^{th} sire in the l^{th} set; β_{jl} is the effect of the j^{th} dam in the l^{th} set; δ_{lm} is the effect of the m^{th} shift of the l^{th} set; Y_l is the effect of the l^{th} set; $(\alpha\beta)_{ijl}$ is the interaction of the i^{th} sire mated to the j^{th} dam in the l^{th} set; $(\alpha\delta)_{ilm}$ is effect of i^{th} sire x m^{th} shift interaction in the l^{th} set; $(\beta\delta)_{jlm}$ is the j^{th} dam x m^{th} shift interaction in the l^{th} set; e_{ijklm} is the environmental and remainder of the genetic deviations.

$i = 1,2.....I$ sires

$j = 1,2.....J$ dams

$m = 1,2.....M$ shifts. There is the same number of shifts as sires in a set.

$l = 1,2.....L$ sets

The first analysis uses the means of full sib families.

Analysis of Variance - 1

Using means of full-sib progeny

Source	d.f.	M.S.	EMS
Sets	$L - 1$	MS_L	
Sires w/sets	$L(I - 1)$	MS_S	$n_k\sigma_W^2 + \sigma_{SD}^2 + k_6\,\sigma_{SM}^2 + \sigma_{DM}^2 + k_7\,\sigma_S^2$
Dams w/sets	$L(J - 1)$	MS_D	$n_k\sigma_W^2 + \sigma_{SD}^2 + k_4\,\sigma_{SM}^2 + \sigma_{DM}^2 + k_5\,\sigma_D^2$
Shifts w/sets	$L(I - 1)$	MS_M	$n_k\sigma_W^2 + \sigma_{SD}^2 + k_2\,\sigma_{SM}^2 + \sigma_{DM}^2 + k_3\,\sigma_M^2$
Residual w/sets	$L(I - 1)$ $(J - 2)$	MS_I	$n_k\sigma_W^2 + \sigma_{SD}^2 + k_1\,\sigma_{SM}^2 + \sigma_{DM}^2$

$k_1 = J(I - 2)/_{I(J - 2)}$
$k_2 = k_6 = J/_I$
$k_3 = k_7 = J$
$k_4 = J(I - 1)/_{I(J - 1)}$
$k_5 = I$

$$n_k = \frac{1}{IJL} \sum_i \sum_j \sum_l \frac{1}{n_{ijl}} \qquad \text{(Reciprocal of harmonic mean)}$$

where n_{ijl} = number of full sibs from a mating of the i^{th} sire with the j^{th} dam in the l^{th} set.

A second analysis has to be completed using individual observations.

Analysis of Variance - 2

Individual Observations

Source	d.f.	MS	EMS
Between matings	IJL - 1	not needed	
Between full sibs--progeny w/matings	n...-IJL	MS_W	σ^2_W

n... = total number of progeny

An examination of the EMS of analysis of variance--1 indicates that the interaction dam x shifts (σ^2_{DM}) is confounded with the sire x dam (σ^2_{SD}) interactions in MS_I. If we assume that the shift interactions are negligible then the variance components can be obtained easily.

2. Genetic model

The variance component σ^2_S is equivalent to the covariance of half sibs (sire groups). The component σ^2_D is the covariance of half sibs (dam groups) and contains the maternal effect. The component σ^2_{SD} is the covariance of full sibs minus the half sibs covariance (sires) and half sibs covariance (dams).

The coefficients α and δ are $(F = 0)$:

	α	δ
cov_{HS}	1/4	0
cov_{FS}	2/4	1/4

The $\mathrm{cov}_{HS} = 1/4V_A + 1/16V_{AA} + \ldots\ldots\ldots\ldots$

$\mathrm{cov}_{FS} = 2/4V_A + 1/4V_D + 1/4V_{AA} + 1/8V_{AD} + 1/16\ V_{DD} + 1/8V_{AAA} + \ldots\ldots\ldots\ldots$

$\sigma^2_S = \mathrm{cov}_{HS(S)}$

$\sigma^2_D = \mathrm{cov}_{HS(D)}$

$\sigma^2_{SD} = \mathrm{cov}_{FS} - (\mathrm{cov}_{HS(S)} + \mathrm{cov}_{HS(D)}) = 1/4V_D + 1/8V_{AA} + 1/8V_{AD} +$

$1/16V_{DD} + \ldots\ldots\ldots\ldots$

The component σ^2_W contains the remainder of the genetic variance and the environmental variance or $\sigma^2_T - \mathrm{cov}_{FS}$.

The genetic and environmental interpretation of the components is:

										Heterogametic			
										Males		Females	
	Relatives' Covariance	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E	♂♂ V_L	♀♀ V_L	♂♂ V_L	♀♀ V_L
σ^2_S	$\mathrm{cov}_{HS(S)}$	$\frac{1}{4}$	0	$\frac{1}{16}$	0	0	$\frac{1}{64}$	0	0	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$
σ^2_D	$\mathrm{cov}_{HS(D)}$	$\frac{1}{4}$	0	$\frac{1}{16}$	0	0	$\frac{1}{64}$	1	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	0
σ^2_{SD}	$\mathrm{cov}_{FS} - (\mathrm{cov}_{HS(S)} + \mathrm{cov}_{HS(D)})$	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$	0	0	0	0	0	0
σ^2_W	$\sigma^2_T - \mathrm{cov}_{FS}$	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{7}{8}$	$\frac{15}{16}$	$\frac{56}{64}$	0	1	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$

3. Computational formulas. Z designates the mean of full sib progeny of each mating within a shift and set. The symbol k for individuals does not appear.

Analysis of Variance - 1

Source	Sum of Squares	Mean Squares
Correction term (C.T.)	$\frac{Z^2_{...}}{IJL}$	
Sets	$\sum_l \frac{Z^2_{..l.}}{IJ}$ - C.T.	
Sires w/sets	$\sum_i \sum_l \frac{Z^2_{i.l.}}{J} - \sum_l \frac{Z^2_{..l.}}{IJ}$	$SS_S / L(I-1)$
Dams w/sets	$\sum_j \sum_l \frac{Z^2_{.jl.}}{I} - \sum_l \frac{Z^2_{..l.}}{IJ}$	$SS_D / L(J-1)$
Shifts w/sets	$\sum_l \sum_m \frac{Z^2_{..lm}}{J} - \sum_l \frac{Z^2_{..l.}}{IJ}$	$SS_M / L(I-1)$
Residual w/sets	$\sum_i \sum_j \sum_l Z^2_{ijlm}$ - Sires SS - Dams SS - Shifts SS - $\sum_l \frac{Z^2_{..l.}}{IJ}$	$SS_I / L(I-1)(J-2)$

The second analysis uses individual observations.

Analysis of Variance - 2

Source	Sum of Squares	Mean Squares
Between matings	$\frac{\sum_i \sum_j \sum_l Y^2_{ij.l}}{n_{ijl}}$	
Between full sibs	$\sum_i \sum_j \sum_k \sum_l Y^2_{ijkl} - \frac{\sum_i \sum_j \sum_l Y^2_{ij.l}}{n_{ijl}}$	$SS_W / n... - IJL$

n... = total number of individuals.

Under the assumption of no sire x shift and dam x shift interactions the components are obtained as follows:

$$\sigma_W^2 = MS_W$$

$$\sigma_S^2 = \frac{MS_S - MS_I}{k_7}$$

$$\sigma_D^2 = \frac{MS_D - MS_I}{k_5}$$

$$\sigma_{SD}^2 = MS_I - n_k MS_W$$

The standard error of the components is given by the previous formula on page 17.

The heritabilities are

$$h_S^2 = \frac{4\ \sigma_S^2}{\sigma_S^2 + \sigma_D^2 + \sigma_{SD}^2 + \sigma_W^2}$$

$$h_D^2 = \frac{4\ \sigma_D^2}{\sigma_S^2 + \sigma_D^2 + \sigma_{SD}^2 + \sigma_W^2}$$

The standard errors of the heritabilities are

$$\text{S.E. } (h_S^2) \cong \frac{4\sqrt{\text{var } (\sigma_S^2)}}{\sigma_S^2 + \sigma_D^2 + \sigma_{SD}^2 + \sigma_W^2}$$

$$\text{S.E. } (h_D^2) \cong \frac{4\sqrt{\text{var } (\sigma_D^2)}}{\sigma_S^2 + \sigma_D^2 + \sigma_{SD}^2 + \sigma_W^2}$$

The model given here is similar to that of Miller, et. al 1963 except that shift effects were separated from sire effects in our model. The main point is that with genotype x environment interactions (sire x shifts and dam x shifts) estimation of variance components is affected.

B. Plants

With plants it is not necessary to employ shifts. Sets may or may not be used depending on the experiment. This design is Experiment II of Comstock and Robinson (1952). The replicates are considered fixed with one plot per mating in each replicate. Whether or not replicates should be considered fixed depends upon the experiment. If they are random then a different model has to be used involving genotype x replicate interactions. If these interactions are present then the estimate of cov_{HS} will be inflated and the estimate of non-additive genetic variances will be decreased (Morley, 1960).

Paternal and maternal plants can be randomly chosen from the reference non-inbred population or inbred lines can be mated.

1. Statistical model

There are two analyses because of the difficulty of obtaining equal numbers per plot (see Kempthorne, 1957, pg. 468).

The formula for both analyses is:

$$Y_{hijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + R_h + e_{hijk}$$

where Y_{hijk} = the observation of the k^{th} full sib progeny in a plot in the h^{th} replication of the i^{th} paternal plant and the j^{th} maternal plant. μ is common to all observations, α is the effect of the i^{th} paternal plant, β_j is the effect of the i^{th} paternal plant, $(\alpha\beta)_{ij}$ is the interaction of the paternal and maternal plants, R_h is the effect of the h^{th} replication, and e_{hijk} is the environmental variance and remainder of genetic variance between full sibs on the same plot.

Analysis of Variance - 1

(Means of full sib progeny in each plot)

Source of variation	d.f.	SS	MS	
Replications	R-1	SS_R	MS_R	
Paternal plants	S-1	SS_S	MS_S	$\sigma_c^2 + n_k\sigma_W^2 + R\sigma_{SD}^2 + RD\sigma_S^2$
Maternal plants	D-1	SS_D	MS_D	$\sigma_c^2 + n_k\sigma_W^2 + R\sigma_{SD}^2 + RS\sigma_D^2$
Paternal x maternal	(S-1)(D-1)	SS_{SD}	MS_{SD}	$\sigma_c^2 + n_k\sigma_W^2 + R\sigma_{SD}^2$
Paternal-maternal combinations x replicates	(DS-1)(R-1)	SS_I	MS_I	$\sigma_c^2 + n_k\sigma_W^2$

R = number of replicates
S = number of paternal plants (lines)
D = number of maternal plants (lines)

$$n_k = \frac{1}{RSD} \sum\sum\sum_{hij} \frac{1}{n_{hij}} \qquad \text{(reciprocal of harmonic mean)}$$

where n_{hij} = number of full sibs in the h^{th} replicate from the i^{th} paternal plant (line) crossed to the j^{th} maternal plant (line).

σ_c^2 = environment variance of the differences between plots common to all individuals within a plot.

The variance between individuals of a full sib family on a plot is obtained using the individual records.

Analysis of Variance - 2

(Individual progeny)

Source of Variation	d.f.	SS	MS	EMS
Between plots	RSD-1	SS	--	--
Between full-sib progeny within plots	n... - RSD	SS_W	MS_W	σ_W^2

n... = total number of progeny

2. Genetic model

The variance component σ_S^2 is the covariance of the paternal plants half sibs while σ_D^2 is the covariance of maternal plants' half sib groups. The component σ_{SD}^2 is the covariance of full sibs minus the two half sibs covariances.

If single plants are taken from a non-inbred population or a single plant represents each inbred line so there are paternal lines and maternal lines then the coefficients α and δ are:

	α	δ
cov_{HS}	$\frac{1 + F_S}{4}$	0
cov_{FS}	$\frac{2 + F_S + F_D}{4}$	$\frac{(1 + F_S)(1 + F_D)}{4}$

where F_S is the inbreeding coefficient of the paternal lines and F_D is the inbreeding coefficient of the maternal lines.

The covariance estimates

$$cov_{HS} = \frac{1 + F_S}{4} V_A + \left(\frac{1 + F_S}{4}\right)^2 V_{AA} + \ldots\ldots\ldots$$

$$cov_{FS} = \frac{2 + F_S + F_D}{4} V_A + \frac{(1 + F_S)(1 + F_D)}{4} V_D + \left(\frac{2 + F_S + F_D}{4}\right)^2 V_{AA} +$$
$$\left(\frac{2 + F_S + F_D}{4}\right) \frac{(1 + F_S)(1 + F_D)}{4} V_{AD} + \left[\frac{(1 + F_S)(1 + F_D)}{4}\right]^2 V_{DD} +$$
$$\ldots\ldots\ldots$$

The variance components in terms of the resemblance between relatives are:

$$\sigma^2_S = \mathrm{cov}_{HS(S)}$$

$$\sigma^2_D = \mathrm{cov}_{HS(D)}$$

$$\sigma^2_{SD} = \mathrm{cov}_{FS} - (\mathrm{cov}_{HS(S)} + \mathrm{cov}_{HS(D)})$$

$$\sigma^2_W = \sigma^2_T - \mathrm{cov}_{FS}$$

$$\sigma^2_c = \text{plot environmental variance}$$

When more than six plants represent an inbred line and the inbreeding coefficient is the same over all lines then only analysis of variance -1 is used. The coefficients α and δ are different.

	α	δ
Only one line in common, cov_{A^-,A^-}	$F/2$	0
Two lines in common, $\mathrm{cov}_{AB,AB}$	F	F^2

The components estimate

$$\sigma^2_S = \mathrm{cov}_{A^-,A^-} = F/2\ V_A + (F/2)^2\ V_{AA} + \ldots\ldots..$$

$\sigma^2_D = \mathrm{cov}_{A^-,A^-}$ estimates the same genetic parameters.

$$\sigma^2_{SD} = \mathrm{cov}_{AB,AB} - (\mathrm{cov}_{A^-,A^-} + \mathrm{cov}_{A^-,A^-}) = F^2 V_D +$$

$$7/8\ F^2 V_{AA} + F^3 V_{AD} + F^4 V_{DD} + \ldots\ldots..$$

σ^2_W estimates the remainder of the genetic variance.

When F = 1 it doesn't matter whether one or several plants per line are used because genotypically every individual is the same within a line. The genetic interpretation of the variance components is:

Components	Covariances	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E
σ^2_S	$cov_{HS(S)}$	$\frac{1}{2}$	0	$\frac{1}{16}$	0	0	$\frac{1}{32}$	0	0
σ^2_D	$cov_{HS(D)}$	$\frac{1}{2}$	0	$\frac{1}{16}$	0	0	$\frac{1}{32}$	1	0
σ^2_{SD}	$cov_{FS} - cov_{HS(S)} - cov_{HS(D)}$	0	1	$\frac{14}{16}$	1	1	$\frac{30}{32}$	0	0
σ^2_W	$\sigma^2_T - cov_{FS}$	0	0	0	0	0	0	0	1

3. Computational formulas. When plot means are used Z_{hij} will be the symbol designating the observation. The designation k will not appear.

Analysis of Variance - 1

Source	Sum of Squares	Mean Squares
Correction term (C.T.)	$\frac{Z^2_{...}}{RSD}$	
Replications	$\sum_h \frac{Z^2_{h..}}{SD} - C.T.$	$SS_R / R-1$
Paternal plants	$\sum_i \frac{Z^2_{.i.}}{RD} - C.T.$	$SS_S / S-1$
Maternal plants	$\sum_j \frac{Z^2_{..j}}{RS} - C.T.$	$SS_D / D-1$
Paternal x maternal	$\sum_i \sum_j \frac{Z^2_{.ij}}{R} - \sum_j \frac{Z^2_{..j}}{RS} - \sum_i \frac{Z^2_{.i.}}{RD} + C.T.$	$SS_D / (S-1)(D-1)$
Paternal-maternal combinations x replicates	$\sum_h \sum_i \sum_j Z^2_{hij} - \sum_i \sum_j \frac{Z^2_{.ij}}{R} -$ $\sum_h \frac{Z^2_{h..}}{SD} + C.T.$	$SS_I / (SD-1)(R-1)$

A further analysis is completed between and within plots using the observations on individuals. Y_{hijk} is the symbol.

Analysis of Variance - 2

Source	d.f.	Sum of Squares	M.S.
Between plots	RDS-1	$\underset{hij}{\Sigma\Sigma\Sigma} \frac{Y^2_{hij.}}{n_{hij}} - C.T.$	
Within plots	n...-RDS	$\underset{hijk}{\Sigma\Sigma\Sigma\Sigma} Y^2_{hijk} - \underset{hij}{\Sigma\Sigma\Sigma} \frac{Y^2_{hij.}}{n_{hij}}$	$SS_W / n...-RDS$

n... = total number of individuals

Estimating variance components

$$\sigma^2_S = \frac{MS_S - MS_{SD}}{RD}$$

$$\sigma^2_D = \frac{MS_D - MS_{SD}}{RS}$$

$$\sigma^2_{SD} = \frac{MS_{SD} - MS_I}{R}$$

$$\sigma^2_W = MS_W$$

$$\sigma^2_c = MS_I - n_k MS_W$$

phenotypic variance = $\sigma^2_S + \sigma^2_D + \sigma^2_{SD} + \sigma^2_W$

Whether or not σ^2_c should be included in the phenotypic variances is debatable.

Standard error of the components is the same as on page 17.

$$S.E. \cong \sqrt{\frac{2}{k^2} \sum_g \frac{MS^2_g}{f_g + 2}}$$

4. Example. Four paternal (pollen parent) Western White Pine trees were mated to seven maternal (seed parent) trees and 2,654 progeny grown in plots replicated in four replications, one plot per mating in a replication. The epicotyl length was measured in centimeters and the heritability calculated in a factorial analysis (Hanover & Barnes, 1962). It is assumed that F = 0.

Table 1. Plot means of progeny epicotyl length

Maternal parent	Replication	Paternal parent				$Z_{..j}$
		#17	#19	#22	#58	
#193	1	4.47	3.41	3.52	3.43	
	2	4.32	2.46	4.17	3.36	
	3	3.50	3.65	5.44	4.10	
	4	3.58	2.97	3.81	3.63	
	$Z_{.ij}$	15.87	12.49	16.94	14.52	59.82
#195	1	4.38	3.10	3.27	4.32	
	2	3.32	2.19	3.43	3.23	
	3	3.24	2.69	2.72	3.65	
	4	3.55	2.97	3.38	3.08	
	$Z_{.ij}$	14.49	10.95	12.80	14.28	52.52
#197	1	4.80	2.92	3.76	3.19	
	2	4.74	2.32	3.38	3.73	
	3	5.14	2.97	3.54	3.15	
	4	4.21	2.18	3.38	3.87	
	$Z_{.ij}$	18.89	10.39	14.06	13.94	57.28
#201	1	3.64	2.92	3.26	3.41	
	2	2.86	3.10	4.38	2.96	
	3	2.87	2.48	3.62	3.67	
	4	2.56	2.52	3.75	2.37	
	$Z_{.ij}$	11.93	11.02	15.01	12.41	50.37
#203	1	4.05	4.32	3.46	2.95	
	2	3.73	4.14	3.21	3.17	
	3	4.50	3.59	3.14	2.67	
	4	4.33	3.85	3.11	2.84	
	$Z_{.ij}$	16.61	15.90	12.92	11.63	57.06
#204	1	3.75	2.63	2.83	2.93	
	2	2.34	2.36	3.78	3.20	
	3	4.11	2.27	3.75	2.52	
	4	2.62	2.68	3.29	3.13	
	$Z_{.ij}$	12.82	9.94	13.65	11.78	48.19
#208	1	4.20	3.23	4.45	3.73	
	2	3.31	2.72	3.04	3.31	
	3	4.58	2.38	2.89	3.73	
	4	3.82	2.45	4.20	3.30	
	$Z_{.ij}$	15.91	10.78	14.58	14.07	55.34
$Z_{.i.}$		106.52	81.47	99.96	92.63	$Z_{...} = 380.58$

Replication ($Z_{h..}$)

1	2	3	4
100.33	92.26	96.56	91.43

$R = 4$, $S = 4$, $D = 7$, $RSD = 112$ $\qquad \sum_{hij}\sum\sum Z^2_{hij} = 1,343,593$

Analysis of Variance - 1

Correction term

$$\frac{(380.58)^2}{112} = 1,293.224$$

Replications

$$\frac{(100.33)^2 + (92.26)^2 + (96.56)^2 + (91.43)^2}{28} = 1,295.046$$

$$SS_R = 1,295.046 - 1,293.224 = 1.822$$

Paternal

$$\frac{(106.52)^2 + (81.47)^2 + (99.96)^2 + (92.63)^2}{28} = 1,305.578$$

$$SS_S = 1,305.578 - 1,293.224 = 12.354$$

Maternal

$$\frac{(59.82)^2 + \ .\ .\ .\ + (55.34)^2}{16} = 1,299.722$$

$$SS_D = 1,299.722 - 1,293.224 = 6.498$$

Paternal x maternal

$$\frac{(15.87)^2 + (12.49)^2 + \ldots + (14.58)^2 + (14.07)^2}{4} = 1,325.537$$

$$SS_{SD} = 1,325.537 - 1,299.722 - 1,305.578 + 1,293.224 = 13.461$$

Paternal-maternal combinations x replicates

$$SS_I = 1,343.593 - 1,325.537 - 1,295.046 + 1,293.224 = 16.234$$

Source	d.f.	Sum of Squares	Mean Squares
Replications	4 - 1 = 3	1.822	0.607
Paternal	4 - 1 = 3	12.354	4.118
Maternal	7 - 1 = 6	6.498	1.083
Paternal x maternal	3 x 6 = 18	13.461	0.748
Paternal-maternal combinations x replicates	(28 - 1)(3) = 81	16.234	0.200

Individual observations on 2,654 trees were analyzed below.

Analysis of Variance - 2

Source	Sum of Squares	d.f.	Mean Squares
Between plots	32,867.24 - 31,651.37 = 1,215.87	112-1 = 111	--
Between individuals, within plots	35,685.85 - 32,867.24 = 2,818.61	2,654 - 112 = 2,542	1.109

$$n_k = \frac{1}{112}\left(\frac{1}{27} + \ . \ . \ . + \frac{1}{5}\right) = 0.0461$$

Obtaining variance components

$$\sigma_S^2 = \frac{4.118 - 0.748}{28} = 0.120$$

$$\sigma_D^2 = \frac{1.083 - 0.748}{16} = 0.0209$$

$$\sigma_{SD}^2 = \frac{0.748 - 0.200}{4} = 0.137$$

$$\sigma_W^2 = 1.109$$

$$\sigma_c^2 = 0.200 - 0.0461\ (1.109) = 0.149$$

Phenotypic variance = 0.120 + 0.0209 + 0.137 + 1.109 = 1.3869

Standard errors of the components

$$\text{S.E. } (\sigma_S^2) \cong \sqrt{\frac{2}{28^2}\left(\frac{4.118^2}{5} + \frac{0.748^2}{20}\right)} \cong 0.093$$

$$\text{S.E. } (\sigma_D^2) \cong \sqrt{\frac{2}{16^2}\left(\frac{1.083^2}{8} + \frac{0.748^2}{20}\right)} \cong 0.037$$

$$\text{S.E. } (\sigma_{SD}^2) \cong \sqrt{\frac{2}{4^2}\left(\frac{0.748^2}{20} + \frac{0.200^2}{83}\right)} \cong 0.060$$

Heritability estimates if the individual trees that were measured were mated together would be:

$$h_S^2 = \frac{4\ \sigma_S^2}{\sigma_T^2} = \frac{4(0.120)}{1.3869} = 0.346$$

$$h_D^2 = \frac{4\ \sigma_D^2}{\sigma_T^2} = \frac{4(0.0209)}{1.3869} = 0.060$$

$$h_{D+S}^2 = \frac{2(\sigma_S^2 + \sigma_D^2)}{\sigma_T^2} = \frac{2(0.120 + 0.0209)}{1.3869} = 0.203$$

If genotype x environment interactions are present then these estimates are inflated in the following way (Dickerson, 1963):

Test	Performance of Progeny	h^2
One environment	Same environment	$\frac{V_A + V_{GE}}{V_A + V_D + V_{GE} + V_E}$
One environment	Other environments	$\frac{V_A}{V_A + V_D + V_{GE} + V_E}$

Standard errors of the heritabilities

$$\text{S.E. } (h_S^2) = \frac{4\ (0.093)}{1.3869} = 0.268$$

$$\text{S.E. } (h_D^2) = \frac{4\ (0.037)}{1.3869} = 0.107$$

IV. Diallel Crosses

A set of p lines are crossed amongst themselves. There would be p^2 crosses dividing into three portions: the p lines, a group of 1/2 p (p-1) F_1's and the reciprocal 1/2 p (p-1) F_1's. Griffing (1956) has given the models for four methods: (1) all possible p crosses, (2) parental lines and one set of F_1's, (3) one set of F_1's and the reciprocal set, and (4) one set of F_1's.

A. Animals

Here one set of F_1's and its reciprocal will be analyzed. The mean of the crosses will be used in one analysis and the individuals within crosses in another analysis.

1. Statistical model

$$Z_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + e_{ij}$$

where Z_{ij} is the mean of the cross between line i (when used as a sire) and line j (when used as the dam), μ is overall mean, g_i is the general combining ability of the i^{th} line, g_j is general combining ability of the line j, s_{ij} is the interaction of the i^{th} and j^{th} lines $(i + j)$, r_{ij} is the reciprocal effect of the ij^{th} versus the ji^{th} cross and e_{ij} is the random error.

Two models are considered. In Model I the lines are fixed while in Model II the lines are a random sample. Although it is possible, it would be relatively rare that lines of animals would meet the assumptions for a Model II analysis (all inbred lines derived from the same non-inbred reference populations, no selection of lines, same inbreeding in each of the lines).

The animals of each line are mated at random with animals of each of the other lines.

Using the means of each cross Analysis of Variance -1 presents the expected mean squares for Models I and II.

ANALYSIS OF VARIANCE - 1

				Expected Mean Squares	
Source	d.f.	SS	MS	Model I	Model II
GCA	p-1	SS_{gca}	MS_{gca}	$n_k\sigma_W^2 + 2\,(p-2)\left[\frac{1}{(p-1)}\right]\Sigma g_i^2$	$n_k\sigma_W^2 + 2\,\sigma_{sca}^2 + 2\,(p-2)\,\sigma_{gca}^2$
SCA	p(p-3)/2	SS_{sca}	MS_{sca}	$n_k\sigma_W^2 + 2\left[\frac{2}{p(p-3)}\right]\sum_{i<j}\sum s_{ij}^2$	$n_k\sigma_W^2 + 2\,\sigma_{sca}^2$
Reciprocal	p(p-1)/2	SS_r	MS_r	$n_k\sigma_W^2 + 2\,\frac{2}{p(p-1)}\sum_{i<j}\sum r_{ij}^2$	$n_k\sigma_W^2 + 2\,\sigma_r^2$

n_k = reciprocal of harmonic mean of individuals within a cross

$$= \frac{1}{p(p-1)} \sum_{i}\sum_{\substack{j \\ i \neq j}} \frac{1}{n_{ij}}$$

where n is the number of animals in the ij^{th} and ji^{th} crosses.

The second analysis uses individual data. If individual data are not available (pen means, etc.) then ANOVA-1 is used alone. The second analysis estimates σ^2_W.

The formula is $Y_{fk} = \mu + C_f + e_{fk}$

where Y_{fk} is the individual observation of the k^{th} progeny in the f^{th} cross, μ is the general mean, C is the effect of the f^{th} cross, and e_{fk} is the environmental and genetic variance among individuals within crosses.

ANALYSIS OF VARIANCE - 2
(Individual data)

Source	d.f.	MS	Expected Mean Squares
Crosses	$p(p-1)-1$	MS_c	-- --
Individuals within crosses	$n..-p(p-1)$	MS_W	σ^2_W

n.. = total number of individuals

See Eisen *et al*. (1967) for an analysis where crosses were made over several years.

2. Genetic model

In Model I estimates of the parameter g_i involves the accumulative additive genetic effects of autosomal genes of line i, plus some sex linked and maternal effects, s_{ij} is the cumulative non-additive genetic effect of the cross ij and ji, r_{ij} is the reciprocal effect and with animals contains mainly maternal and sex linked effects.

In Model II if we assume that the lines are completely inbred then estimates of the variance components have the following genetic meaning:

									Heterogametic			
									Males		Females	
									♂♂	♀♀	♂♂	♀♀
Components	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E	V_L	V_L	V_L	V_L
σ^2_{gca}	1	0	1	0	0	1	1/4	0	1/4	1	1	1/4
σ^2_{sca}	0	1	0	1	1	0	0	0	0	0	0	0
σ^2_r	0	0	0	0	0	0	1/2	0	1/2	0	0	1/2
σ^2_W	0	0	0	0	0	0	0	1	0	0	0	0

Heterogametic males include mammals and insects, heterogametic females include birds. The genetic interpretation of this design is discussed by Eisen, et al. (1966). Note that the general combining ability variance includes estimates of maternal variance. Designs incorporating general and specific reciprocal variances have been given by Cockerham (1963) and Eisen, et al. (1967). There are some differences concerning the interpretation of the effects.

When the lines are not completely inbred the variance components estimate less of the genetic variance.

3. Computational formulas

The symbol Z designates the mean of the specific cross.

Analysis of Variance - 1

Source of Variation	Sum of Squares
GCA	$\frac{1}{2(p-2)} \Sigma (Z_{i.} + Z_{.i})^2 - \frac{2Z_{..}^2}{p(p-2)}$
SCA	$\frac{1}{2} \underset{i<j}{\Sigma\ \Sigma} (Z_{ij} + Z_{ji})^2 - \frac{1}{2(p-2)} \Sigma (Z_{i.} + Z_{.i})^2 + \frac{1}{(p-1)(p-2)} Z_{..}^2$
Reciprocal	$\frac{1}{2} \underset{i<j}{\Sigma\ \Sigma} (Z_{ij} - Z_{ji})^2$

The second analysis utilizes the individual observations.

Analysis of Variance - 2

Source of Variation	Sum of Squares	Mean Square
Crosses	$\sum_f Y_{f.}^2 - C.T.$	Not needed
Individuals within crosses	$\sum_f \sum_k Y_{fk}^2 - \sum_f Y_{f.}^2$	$SS_W / [n_{..} - p(p-1)]$

Estimating variance components in Model II

$$\sigma_W^2 = MS_W$$

$$\sigma_r^2 = \frac{MS_s - n_k\ MS_W}{2}$$

$$\sigma_{sca}^2 = \frac{MS_{sca} - n_k\ MS_W}{2}$$

$$\sigma_{gca}^2 = \frac{MS_{gca} - MS_{sca}}{2(p-2)}$$

B. Plants

The most common diallel cross in plants consists of one set of F_1's. It will be assumed that p lines are inbred and that all of them have the same coefficient of inbreeding. It is possible to mate random individuals from a reference population but the usual situation is a group of lines selected for some trait such as yield.

1. Statistical model

$$Z_{ij} = \mu + g_i + g_j + s_{ij} + e_{ij}$$

where Z_{ij} = mean performance of the i^{th} parental line mated to the j^{th} parental line. μ is common to all observations, g_i (g_j) is the general combining ability of the i^{th} (j^{th}) parental line. s_{ij} is the interaction of the i^{th} and j^{th} parents, and e_{ij} is the random error.

Using the means of the crosses, the first analysis of variance is given for two sampling assumptions, Model I and Model II.

Analysis of Variance - 1

Source	d.f.	SS	MS	EMS	
				Model I	Model II
GCA	p-1	SS_{gca}	MS_{gca}	$n\sigma_W^2 + (p-2)(\frac{1}{p-1}) \sum_i g_i^2$	$n\sigma_W^2 + \sigma_{sca}^2 + (p-2)\ \sigma_{gca}^2$
SCA	p(p-3)/2	SS_{sca}	MS_{sca}	$n\sigma_W^2 + \left(\frac{2}{p(p-3)}\right) \sum\sum_{i<j} s_{ij}^2$	$n\sigma_W^2 + \sigma_{sca}^2$

n = reciprocal of average number of plants per cross. With unequal numbers of plants use the reciprocal of the harmonic mean.

The second analysis of variance is used where individual data are available. The formula is

$$Y_{hfk} = \mu + \delta_h + \chi_f + (\delta\chi)_{hf} + e_{hfk}$$

where Y_{hfk} = the observation of the k^{th} individual of the f^{th} cross in the h^{th} replicate. μ is common to all observations, δ_h is effect of the h^{th} replicate, χ_f is effect of f^{th} cross, $(\delta\chi)_{hf}$ is interaction h^{th} replicate and f^{th} cross and e_{hfk} is the genetic and environmental effect between full sibs in a plot. There is only one plot per cross within a replicate.

Analysis of Variance - 2 (observations on individuals)

Source	d.f.	SS	MS	EMS	
				Model I	Model II
Replications	R - 1	SS_R	MS_R	$\sigma_W^2 + FK\phi(R)$	$\sigma_W^2 + K\,\sigma_{RF}^2 + FK\sigma_R^2$
Crosses (F_1's)	F - 1	SS_F	MS_F	$\sigma_W^2 + RK\phi(F)$	$\sigma_W^2 + K\,\sigma_{RF}^2 + RK\sigma_F^2$
Crosses x replications	(R-1)(F-1)	SS_{RF}	MS_{RF}	$\sigma_W^2 + K\,\phi\,(RF)$	$\sigma_W^2 + K\,\sigma_{RF}^2$
Between full sibs within plots	RF(K-1)	SS_W	MS_W	σ_W^2	σ_W^2

R = number of replications
F = number of crosses (F_1's)
K = number of full sibs within a plot

It is possible to consider mixed models where replications are random with crosses fixed and vice versa. Griffing (1956) gives some of these models.

To estimate n and error term σ_W^2 in ANOVA - 1 for Model I assumptions, use 1/RK and utilize MS_W. For Model II assumptions use n = 1/RK and MS_{RF}. These error terms are then on the basis of means.

2. Genetic model. Model II assumptions (see Matzinger and Kempthorne, 1956)

If only one plant is used per line, then the coefficients α and δ are:

	α	δ
cov_{HS}	$\frac{1+F}{4}$	0
cov_{FS}	$\frac{1+F}{2}$	$\left(\frac{1+F}{2}\right)^2$

The covariance of half sibs estimates

$$cov_{HS} = \frac{1+F}{4}\;V_A + \left(\frac{1+F}{4}\right)^2 V_{AA} + \ldots\ldots.$$

and the covariance of full sibs estimates

$$cov_{FS} = \frac{1+F}{2}\;V_A + \left(\frac{1+F}{2}\right)^2 V_D + \left(\frac{1+F}{2}\right)^2 V_{AA} + \left(\frac{1+F}{2}\right)^3 V_{AD} + \left(\frac{1+F}{2}\right)^4 V_{DD} + \ldots\ldots\ldots\ldots\ldots$$

The variance components in terms of the covariances between relatives are

$$\sigma^2_{gca} = \mathrm{cov}_{HS}$$

$$\sigma^2_{sca} = \mathrm{cov}_{FS} - 2\,\mathrm{cov}_{HS}$$

σ^2_{c} = the common environment of a plot

$$\sigma^2_{W} = \sigma^2_{T} - \mathrm{cov}_{FS}$$

When more than six plants are used per inbred line and the pollen is bulked, the coefficients α and δ are:

	α	δ
$\mathrm{cov}_{A-,A-}$	$F/2$	0
$\mathrm{cov}_{AB,AB}$	F	F^2

The components estimate

$$\sigma^2_{gca} = \mathrm{cov}_{A-,A-} = F/2\ V_A + (F/2)^2\ V_{AA} + \ldots\ldots\ldots$$

$$\sigma^2_{sca} = \mathrm{cov}_{AB,AB} - 2\mathrm{cov}_{A-,A-} = F^2V_D + 7/8\ F^2V_{AA} + F^3V_{AD} + F^4V_{DD} + \ldots\ldots.$$

3. Computational formulas

<u>Analysis of Variance - 1</u>
(using means Z_{ij})

Source	Sum of Squares
G.C.A.	$\frac{1}{p-2} \sum_i Z^2_{i.} - \frac{4}{p(p-2)} Z^2_{..}$
S.C.A.	$\sum\sum_{i<j} Z^2_{ij} - \frac{1}{p-2} \sum_i Z^2_{i.} + \frac{2}{(p-1)(p-2)} Z^2_{..}$

Analysis of Variance - 2
(using individual observations)

Source	Sum of Squares	MS
Correction term	$\frac{Y^2_{...}}{RFK}$	
Replications	$\sum_h \frac{Y^2_{h..}}{FK} - C.T.$	
Crosses (F_1's)	$\sum_f \frac{Y^2_{.f.}}{RK} - C.T.$	
Replications x crosses	$\sum_h \sum_f \frac{Y^2_{hf.}}{K} - \sum_h \frac{Y^2_{h..}}{FK} - \sum_f \frac{Y^2_{.f.}}{RK} + C.T.$	MS_{RF}
Between full sibs, within plots	$\sum_h \sum_f \sum_k Y^2_{hfk} - \sum_h \sum_f \frac{Y^2_{hf.}}{K}$	MS_W

a. Model I

$$n\sigma^2_w = MS_W/RK$$

Estimating General Combining Ability of the i^{th} line.

$$g_i = \frac{1}{p\ (p-2)} \left[p\ Z_{i.} - 2Z_{..} \right]$$

Estimating variance of GCA of the i^{th} line.

$$\sigma^2_{g_i} = (g_i)^2 - \frac{p-1}{p(p-2)}\ n\sigma^2_W$$

Estimating s_{ij} for each cross (F_1)

$$s_{ij} = \underset{i \neq j}{Z_{ij}} - \frac{1}{p-2}\ (Z_{i.} + Z_{.j}) + \frac{2}{(p-1)(p-2)}\ Z_{..}$$

Estimating variance of Specific Combining Ability of i^{th} line.

$$\sigma^2_{s_i} = \frac{1}{(p-2)} \sum_{i \neq j} s^2_{ij} - \frac{p-3}{p-2}\ n\sigma^2_W$$

b. Model II

$$n\sigma^2_W = MS_{RF}/RK$$

$$\sigma^2_{sca} = MS_{sca} - MS_{RF}/RK$$

$$\sigma^2_{gca} = \frac{MS_{gca} - MS_{sca}}{p-2}$$

Approximate standard errors for these components

$$S.E. \cong \sqrt{\frac{2}{k^2} \frac{MS^2_g}{f_g + 2}}$$

where k = coefficient of the variance component being estimated, MS_g = the g^{th} mean square used to estimate the variance component, and f_g = the degrees of freedom of the g^{th} mean square. Estimating the S.E. of σ^2_{gca}

$$S.E. (\sigma^2_{gca}) \cong \sqrt{\frac{2}{(p-2)^2} \left(\frac{MS^2_{gca}}{p+1} + \frac{MS^2_{sca}}{2+p(p-3)/2} \right)}$$

4. Example. The worked example for nine inbred lines of _Zea mays_ in Griffing (1956) is presented with permission of the author and the Australian Journal of Biological Sciences. Total yield is the trait considered and the experimental design was six randomized blocks. The F_1 plots in each block contained 13 plants. The means for total yield for each cross are given below.

Inbred Line Number	Inbred Line Number 2	3	4	5	6	7	8	9	$Z_{i.}$
1	240.0	260.0	230.4	257.0	241.5	266.9	240.1	300.4	2,036.3
2		209.0	217.3	233.1	229.5	266.9	216.3	214.2	1,826.3
3			183.7	253.7	250.1	268.8	222.3	252.1	1,899.7
4				233.8	213.7	255.7	197.4	281.0	1,813.0
5					206.8	272.2	242.9	260.8	1,960.3
6						261.8	270.3	283.9	1,957.6
7							273.2	302.2	2,167.7
8								259.8	1,922.3
9									2,154.4

$Z_{..}$ = 8,868.8
p = 9
example of $Z_{i.}$

$Z_{6.}$ (see line) = 241.5 + 229.5 + 250.1 + 213.7 + 206.8 + 261.8 + 270.3 + 283.9 = 1,957.6.

Calculating Analysis of Variance - 1

Source	Computations
GCA	$\frac{1}{9-2}$ $(2,036.3^2 + 1,826.3^2 + \ldots\ldots + 2,154.4^2)$
	$= \frac{1}{7}$ $(35,088,292.26) = 5,012,613.1$
	$\frac{4}{9(9-2)}$ $(8,868.8)^2 = 4,994,007.20$
	$5,012,613.1 - 4,994,007.2 = 18,605.9 = SS_{gca}$
	$MS_{gca} = 18,605.9/8 = 2,325.7$
SCA	$240.0^2 + 260.0^2 + \ldots\ldots + 259.8^2 = 2,212,649.0$
	$\frac{2}{(9-1)(9-2)}$ $(8,868.8)^2 = 2,809,129.0$
	$2,212,649.0 - 5,012,613.1 + 2,809,129.0 = 9,164.9 = SS_{sca}$
	$MS_{sca} = 9,164.9/27 = 339.4$

Analysis of Variance - 2 has been calculated and is given by Griffing (1956).

Source	d.f.	M.S.
Replications (blocks)	5	257,943.53
Crosses (F_1's)	35	61,889.36
Replications x crosses	175	11,803.61
Between full sibs	2558	1,642.48

The degrees of freedom for between full sibs should be 2592 but was reduced because of missing data.

$n = 1/RK = 1/\text{number of replication} \times \text{number of plants per plot} = 1/(6x13) = 1/78.$

For Model I, estimates are obtained as follows:

Source	d.f.	Mean Square
GCA	(9 - 1) = 8	2,325.7
SCA	9 (9 - 2)/3 = 27	339.4
Error Term	2558	21.05

The error term is 1,642.48/78 = 21.05.

The components

$$\Sigma g_i^2 = (MS_{gca} - MS_W/78)/(\frac{9-2}{9-1})$$

$$= (2,325.7 - 21.05)/\frac{7}{8} = 2,633.88$$

$$\underset{i>j}{\Sigma\ \Sigma} s_{ij}^2 = (MS_{sca} - MS_W/78)/(\frac{2}{9\ (9-3)})$$

$$= (339.4 - 21.05)/\frac{2}{54} = 8,595.5$$

Estimating general combining ability g_i of each line

$$g_i = \frac{1}{9(9-2)}\ [9Z_{i.} - 2\ (8,868.8)]$$

for line 1

$$g_1 = \frac{1}{63}\ [9\ (2,036.3) - 2\ (8,868.8)]$$

$$= 9.35$$

The variance of the GCA of a line

For line 1

$$\sigma_{g_1}^2 = (9.35)^2 - \frac{9-1}{9(9-2)}\ (21.05)$$

$$= 84.78$$

The general combining ability of the lines

Line	g_i	$\sigma^2_{g_i}$
1	9.35	84.78
2	-20.65	423.75
3	-10.16	100.56
4	-22.55	505.83
5	- 1.51	-0.40
6	- 1.89	0.90
7	28.12	788.06
8	- 6.43	45.36
9	26.22	684.82

Estimating specific combining ability for each cross

For cross 1 x 2

$$s_{12} = 240.0 - \frac{1}{9-2}(2{,}036.3 + 1{,}826.3) + \frac{2}{(9-1)(9-2)}\,8{,}868.8 = 4.94$$

The specific combining ability for each cross is given below

Line Number	Line Number 2	3	4	5	6	7	8	9
1	4.94	14.46	-2.76	2.80	-12.31	-16.93	-8.67	18.47
2		-6.54	14.14	8.90	5.68	13.07	-2.47	-37.73
3			-29.94	19.01	15.80	4.48	-6.96	-10.31
4				11.50	-8.21	3.77	-19.47	30.97
5					-36.16	-0.77	4.99	-10.27
6						-10.78	32.77	13.22
7							5.66	1.50
8								-5.85
9								

The specific combining ability variance for line 1

$$\sigma^2_{s_1} = \frac{1}{(9-2)}(4.94^2 + 14.46^2 + \ldots\ldots 18.47^2) - \frac{9-3}{9-2}(21.05) = 139.60$$

The sca variance for the lines

Line	$\sigma^2_{s_i}$
1	139.60
2	264.69
3	258.26
4	361.40
5	270.42
6	435.28
7	73.80
8	221.08
9	431.51

Under Model II assumptions

Source	d.f.	Mean Square
GCA	8	2325.75
SCA	27	339.44
Error	175	151.33

$$\sigma^2_{gca} = \frac{2,325.7 - 339.4}{9-2} = 283.76$$

$$\text{S.E.}(\sigma^2_{gca}) \cong \sqrt{\frac{2}{7^2}\left(\frac{2,325.7^2}{10} + \frac{339.4^2}{29}\right)}$$

$$\cong \sqrt{22,239} = 149.12$$

$$\sigma^2_{sca} = 339.4 - 151.3 = 188.11$$

$$\text{S.E. }(\sigma^2_{sca}) \cong \sqrt{\frac{2}{1}\left(\frac{339.4^2}{29} + \frac{151.3^2}{177}\right)}$$

$$\cong \sqrt{8,202.96} = 90.57$$

The estimate of the additive genetic variance, assuming the additive x additive interactions to be zero, is

$$V_A = 2\,\sigma^2_{gca} = 2\ (283.76 \pm 149.12) = 567.52 \pm 298.24$$

The estimate of the dominance variance, assuming the higher order interactions to be zero, is

$$V_D = \sigma^2_{sca} = 188.11 \pm 90.57$$

The environmental variance between plants on the same plot is

$$V_E = \sigma^2_W = 1,642.48$$

The S.E. is

$$\text{S.E.} = \sqrt{\frac{2}{1}\ \frac{1642.48^2}{2558+2}} = \sqrt{2107.61} = 45.91$$

$$V_E = 1,642.48 \pm 45.91$$

C. Diallel designs utilizing parental information

Completely inbred, partially inbred or random-mating varieties, provided the last two types have reached a Hardy-Weinberg equilibrium, can contribute considerable information about heterosis when the parental lines are reproduced. A general model has been proposed by Gardner and Eberhart (1966) and Eberhart and Gardner (1966).

With $p \geq 4$ and one set of F_1's and the parental line data their analysis is:

Source	d.f.
Populations	$[p(p-1)/2] - 1$
Varieties	$p - 1$
Heterosis (h_{ij})	$p(p-1)/2$
Average ($\bar{h}$)	1
Variety (h_j)	$p - 1$
Specific (s_{ij})	$p(p-3)/2$

where

h_{ij} = heterosis due to differences in gene frequency between i and j varieties and to dominance.

$\bar{h}$ = average heterosis contributed by the particular set of varieties used in the crosses.

h_j = average heterosis contributed by variety j in its crosses measured by the deviation from average heterosis.

s_{ij} = the specific heterosis when variety i is mated to variety j.

Required is the restriction that

$$\sum_i s_{ij} = \sum_j s_{ij} = 0$$

When the selfed progenies of the varieties and/or the selfed progenies of the crosses, the random-mated varieties, the variety crosses random mated, and the variety crosses are available then the following information can be obtained:

Source	d.f.
Populations	$[p(3p+1)/2]-1$
Additive Effects	$n-1$
Dominance Effects	n
Heterosis (H_{ij})	$p(p-1)/2$
Average (h)	1
Variety (h_j)	$p-1$
Specific (s_{ij})	$p(p-3)/2$
Residual	$p(p-1)$

Model I assumptions hold throughout and certain of the parameters are non-orthogonal requiring a computer to provide the least square estimates.

REGRESSION OF OFFSPRING ON PARENT AND HERITABILITY

The reference population is the population from which the parents are derived. The symbol X will denote the observation on the parent. When the mean of the offspring is used Z will be the symbol. It is assumed that the population is not inbred and randomly mated. If the parents are assortatively mated see Reeve, 1952; Dawson, 1964; Wilson et al. 1966.

I. Sire--offspring mean

This design is useful when a sire is mated to a series of dams and each dam has one progeny.

A. Statistical model

$$Z_i = \beta X_i + e_i$$

where Z_i is the mean of the offspring of the i^{th} sire, X is the observation in the i^{th} sire, β is the regression of Z on X and e_i is the error associated with the Z's.

B. Genetic model

The model is given in terms of the covariance of Z and X, cov_{XZ}.

									Heterogametic			
									Males		Females	
Source	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E	♂♂ V_L	♀♀ V_L	♂♂ V_L	♀♀ V_L
cov_{XZ}	$\frac{1}{2}$	0	$\frac{1}{4}$	0	0	$\frac{1}{8}$	0	0	0	1	$\frac{1}{2}$	$\frac{1}{2}$

C. Computational formulas

1. Obtain Σz^2, Σx^2 and Σxz

$$\Sigma z^2 = \Sigma Z^2 - \frac{(\Sigma Z)^2}{N}$$

$$\Sigma x^2 = \Sigma X^2 - \frac{(\Sigma X)^2}{N}$$

$$\Sigma xz = \Sigma XZ - \frac{(\Sigma X)(\Sigma Z)}{N}$$

where N = number of sire - offspring pairs

$$\text{cov}_{XZ} = \frac{\Sigma\ XZ}{N - 1}$$

The regression of offspring on parent (b)

$$b = \frac{\text{cov}_{xz}}{\sigma_x^2} = \frac{\Sigma xz}{x^2}$$ (because N - 1 is common to both numerator and denominator)

2. Heritability

Twice the regression is heritability. $h^2 = 2b$

3. Standard error

$$s_b^2 = \frac{\Sigma z^2 - \frac{(\Sigma xz)^2}{\Sigma x^2}}{N - 2}$$

$$\text{S.E.}(b) = \sqrt{\frac{s_b^2}{\Sigma x^2}}$$

$$\text{S.E.}(h^2) = 2\ \text{S.E.}(b)$$

D. Example: Seventeen chicken sires were mated and the progeny weighed at eight weeks of age. The 8-week weights of the sires and the mean of male progeny are as follows:

Sire weight X	Progeny weight Z	Sire weight X	Progeny weight Z
601	910	882	994
733	983	895	1,030
793	976	952	1,021
795	1,050	953	1,078
818	1,080	961	964
838	1,040	979	976
854	1,040	995	1,110
880	1,025	997	1,041
		1,040	1,035

$\Sigma X = 14{,}966 \qquad N = 17$

$\Sigma X^2 = 13{,}375{,}506$

$$\Sigma x^2 = 13{,}375{,}506 - \frac{(14{,}966)^2}{17} = 200{,}144$$

$\Sigma XZ = 601 \text{ x } 910 + 733 \text{ x } 983 + \ldots\ldots 1{,}040 \text{ x } 1{,}035 = 15{,}319{,}806$

$\Sigma Z = 17{,}353$

$$\frac{(\Sigma X)(\Sigma Z)}{N} = \frac{(14{,}966)(17{,}353)}{17} = 15{,}276{,}764$$

$\Sigma xz = 15{,}319{,}806 - 15{,}276{,}764 = 43{,}042$

$$\text{cov}_{xz} = \frac{43{,}042}{16} = 2{,}690$$

$$b = \frac{43{,}042}{200{,}144} = 0.215$$

$h^2 = 2b = 0.430$

Standard error

$\Sigma Z = 17{,}353$

$\Sigma Z^2 = 17{,}752{,}029$

C.T. $= 17{,}713{,}329$

$\Sigma z^2 = 17{,}752{,}029 - 17{,}713{,}329 = 38{,}700$

$$s_b^2 = \frac{38{,}700 - \frac{(43{,}042)^2}{200{,}144}}{15} = 1{,}963$$

$$\text{S.E. }(b) = \sqrt{\frac{1{,}963}{200{,}144}} = 0.099$$

$\text{S.E. }(h^2) = 2(0.099) = 0.198$

Heritability estimate

$h^2 = 0.43 \pm 0.198$

II. Intra-sire regression of offspring on dam.

With certain species one sire can mate with several dams and each dam produce several offspring.

The sire effect is removed by obtaining the regression of offspring on dam within the sire.

A. Use of mean of dam's offspring

The symbol Z is used to designate the offspring mean while the symbol Y will designate the record on the individual offspring. X will designate the dam's record.

1. Statistical model

$$Z_{ij} - \alpha_i = \mu + \beta\ (X_{ij} - \bar{x}..) + e_{ij}$$

where Z_{ij} is the mean of the records of the offspring from a mating of the i^{th} sire to the j^{th} dam; μ = common mean; α_i = the effect of the i^{th} sire; β is the regression coefficient of Z on X; X_{ij} is the record on the j^{th} dam mated to the i^{th} sire; $\bar{x}..$ is the phenotypic mean; e_{ij} = the deviation of the means of the progeny. The regressions from the sire families are pooled to obtain the common regression coefficient, β.

2. Genetic model

It is assumed that the population is not inbred.

									Heterogametic			
									Males		Females	
									♂♂	♀♀	♂♂	♀♀
	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}	V_M	V_E	V_L	V_L	V_L	V_L
$cov_{D(ZX)}$	$\frac{1}{2}$	0	$\frac{1}{4}$	0	0	$\frac{1}{8}$	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{2}$	1	0

The covariance estimates one-half of the additive genetic variance, so multiplying by two gives an estimate of all V_A. Note that this method also includes the maternal effects V_M.

Dividing the covariance by the variance of the dams, within sires, gives the regression. Twice the regression estimates heritability.

3. Computational formulas

The sum of squares for between dams, within sire are needed for X, Z and XZ. The table below gives the required estimates, $SS_{D(XX)}$, $SCP_{D(ZX)}$, $SS_{D(ZZ)}$. SCP is Sum of Cross Products.

Source	d.f.	Sum of products Dams XX	 Dam x Progeny XZ	 Progeny ZZ
Between sires	S-1	not needed		
Between dams within sires	D-S	$SS_{D(XX)}$	$SCP_{D(ZX)}$	$SS_{D(ZZ)}$
Total	D-1			

where S = no. of sires and D = no. of dams.

a. Analysis of variance for dam's records

Source	Sum of Squares	Symbol
Sires	$\sum_i \frac{X_{i.}^2}{n_i}$	
Dams/sires	$\sum_i \sum_j X_{ij}^2 - \sum_i \frac{X_{i.}^2}{n_i}$	$SS_{D(XX)}$

where n_i is the number of dams mated to the i^{th} sire.

b. The $SS_{D(ZZ)}$ is obtained in the same way using the mean of each dam's progeny, Z.

c. The Sum of Cross Products, $SCP_{D(ZX)}$, is obtained in a similar manner.

Analysis of Covariance

Source	Sum of Cross Products	Symbol
Sires	$\sum_i \frac{X_{i.}\ Z_{i.}}{n_i}$	
Dams/sires	$\sum_i \sum_j X_{ij}\ Z_{ij} - \sum_i \frac{X_{i.}\ Z_{i.}}{n_i}$	$SCP_{D(ZX)}$

$$cov_{D(ZX)} = \frac{SCP_{D(ZX)}}{D - S}$$

d. Regression is obtained

$$b = \frac{SCP_{D(ZX)}}{SS_{D(XX)}}$$

$$h^2 = 2b$$

e. The standard error of h^2

$$s_b^2 = \frac{SS_{D(ZZ)} - \frac{(SCP_{D(ZX)})^2}{SS_{D(XX)}}}{(D-S-1)}$$

$$S.E.(b) = \sqrt{\frac{s_b^2}{SS_{D(XX)}}}$$

$$S.E.(h^2) = 2\,S.E.(b)$$

4. Example: Six sires were mated to differing numbers of dams and the 8-week body weights of the chicken females obtained. The dams' 8-week weight and the mean of the offsprings' records are given.

Sire	Dam (X_{ij})		Progeny mean (Z_{ij})	Sire	Dam (X_{ij})		Progeny mean (Z_{ij})
#1	754		808	#4	969		850
	648		700		849		802
	881		720		732		830
	Σ 2283	$n_i = 3$	2228		Σ 2550	$n_i = 3$	2482
#2	740		725	#5	740		806
	712		840		741		835
	812		800				
	Σ 2264	$n_i = 3$	2365		Σ 1481	$n_i = 2$	1641
#3	765		780	#6	831		830
	807		840		639		800
					733		504
	Σ 1572	$n_i = 2$	1620		Σ 2203	$n_i = 3$	2134

a. Obtaining $SS_{D(XX)}$

Source

Sires $\frac{(2,283)^2}{3} + \frac{(2,264)^2}{3} + \ldots + \frac{(2,203)^2}{3} = 9,563,436$

Dams/sires $(754)^2 + (648)^2 + (881)^2 + (740)^2 + \ldots (733)^2 = 9,643,381$

$9,643,381 - 9,563,436 = 79,945 \quad SS_{D(XX)} = 79,945$

b. Obtaining $SS_{D(ZZ)}$

Source

Sires $$\frac{(2,228)^2}{3} + \frac{(2,365)^2}{3} + \ldots + \frac{(2,134)^2}{3} = 9,749,135$$

Dams/sires $$(808)^2 + (700)^2 + (720)^2 + (725)^2 + \ldots (504)^2 = 9,830,870$$

$$SS_{D(ZZ)} = 81,735$$

c. Obtaining $SCP_{D(ZX)}$

Source

Sires $$\frac{(2,283)(2,228)}{3} + \frac{(2,264)(2,365)}{3} + \ldots + \frac{(2,203)(2,134)}{3}$$

$$= 9,645,541$$

Dams/sires $$(754)\ (808) + (648)\ (700) + \ldots + (733)\ (504) = 9,653,557$$

$$9,653,557 - 9,645,541 = 8,016 \quad SCP_{D(ZX)} = 8,016$$

$$cov_{D(ZX)} = \frac{8,016}{16 - 6} = 801.6$$

The estimate of the additive genetic variance is 2(801.6) = 1,603.

d. Obtaining the regression coefficient

$$b = \frac{8,016}{79,945} = 0.10$$

$$h^2 = 2\ (0.10) = 0.20$$

e. Standard error of h^2

$$s_b^2 = \frac{81,735 - \frac{(8,016)^2}{79,945}}{(16 - 6 - 1)} = 8,992$$

$$S.E.(h^2) = 2\sqrt{0.1125} = 2\ (0.335) = 0.670$$

The heritability estimate is 0.20 ± 0.67.

III. Other methods

The previous two methods are the most common. If the number of offspring per dam is unequal, then other methods may be used. Individual observations of progeny can be regressed on the dam's record (Bohren, et al., 1961).

Another method of obtaining the heritability from the regression is to weight each family (Kempthorne and Tandon, 1953). An explanation of this method with a worked example is given by Falconer (1963).

IV. Correcting for inequality of male and female phenotypic variances. When sire-daughter or dam-son regressions are obtained a correction has to be made because of the differences in the variances of the two sexes. Clayton, et al. (1957) have suggested that the regression coefficient be multiplied by

$$\frac{\sigma ♀}{\sigma ♂}$$

when dam-son regressions are obtained. The σ is the phenotypic standard deviation of the unselected sexes. The standard error of b correspondingly has to be multiplied by this quantity.

CORRELATIONS

The genetic, environmental and phenotypic correlations between two traits can be obtained by methods similar to those used to estimate genetic variances. X will be the symbol for one trait and Y the symbol for the other trait. It will be assumed that the inbreeding of the reference population is zero, although correlations probably can be estimated when inbred lines are crossed using the same assumptions and genetic models as given previously for the estimation of genetic variances.

I. Analysis of variance and covariance

Two designs will be used to estimate correlations, the nested and factorial designs. Diallels can be used in the same way.

A. Nested design

Each sire is mated to several dams each of which produces several offspring.

1. Statistical model

The model is the same as on pages 14 and 23 (plants). The analysis of variance for each trait X and Y separately is the same as given previously. The analysis of covariance between X and Y is as follows:

Analysis of Covariance

Source	d.f.	Mean Cross Products	EMCP
Sires	S-1	MCP_S	$cov_W + k_2\ cov_D + k_3\ cov_S$
Dams	D-S	MCP_D	$cov_W + k_1\ cov_D$
Sibs	n.. - D	MCP_W	cov_W

The components of variance for $\sigma^2_{S(X)}$, $\sigma^2_{S(Y)}$, $\sigma^2_{D(X)}$, $\sigma^2_{D(Y)}$, $\sigma^2_{W(X)}$, $\sigma^2_{W(Y)}$ are obtained as before. The components of covariance can be derived from the above analysis of covariance using the mean cross products.

2. Genetic model (see Mode and Robinson, 1959)

The components of covariance have the following genetic and environmental meaning in terms of genetic covariance between X and Y.

Component of Covariance	Genetic and environmental covariances						
	cov_A	cov_D	cov_{AA}	cov_{AD}	cov_{DD}	cov_{AAA}	cov_E
cov_S	$\frac{1}{4}$	0	$\frac{1}{16}$	0	0	$\frac{1}{64}$	0
cov_D	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{7}{64}$	0
cov_W	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{7}{8}$	$\frac{15}{16}$	$\frac{7}{8}$	1
cov_D+cov_S	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{8}$	0

Thus, cov_S estimates 1/4 additive genetic covariance, 1/16 cov_{AA}, etc.

3. Computational formulas

The components of variance are derived as before. The formulas below refer to obtaining the components of covariance between X and Y.

Analysis of Covariance

Source	Sum of Cross Products	Mean Cross Product
Correction term	$\frac{X_{\cdots}\ Y_{\cdots}}{n_{\cdot\cdot}}$	--
Sires	$\sum_i \frac{X_{i\cdot\cdot}\ Y_{i\cdot\cdot}}{n_{i\cdot}} - \text{C.T.}$	$SCP_S / S-1 = MCP_S$
Dams	$\sum_i \sum_j \frac{X_{ij\cdot}\ Y_{ij\cdot}}{n_{ij}} - \sum_i \frac{X_{i\cdot\cdot}\ Y_{i\cdot\cdot}}{n_{i\cdot}}$	$SCP_D / D-S = MCP_D$
Sibs	$\sum_i \sum_j \sum_k X_{ijk}\ Y_{ijk} - \sum_i \sum_j \frac{X_{ij\cdot}\ Y_{ij\cdot}}{n_{ij}}$	$SCP_W / n_{\cdot\cdot} - D = MCP_W$

Estimating covariance components

$$\mathrm{cov}_W = \mathrm{MCP}_W$$

$$\mathrm{cov}_D = \frac{\mathrm{MCP}_D - \mathrm{MCP}_W}{k_1}$$

$$\mathrm{cov}_S = \frac{\mathrm{MCP}_S - \mathrm{MCP}_D}{k_3}$$

4. Estimation of correlations

The general formula for estimating correlations is

$$r = \frac{\mathrm{cov}_{XY}}{\sqrt{\sigma_X^2 \sigma_Y^2}}$$

Noting the genetic and environmental meaning of the components of variance and covariance the proper covariances and variances are substituted in the general formula.

a. Genetic correlations

1.) Sire components of variance and covariance

$$r_G = \frac{4\ \mathrm{cov}_S}{\sqrt{4\sigma_{S(X)}^2 \quad 4\sigma_{S(Y)}^2}} \qquad \text{(the fours cancel)}$$

The genetic interpretation is

$$r_G = \frac{\mathrm{cov}_A + 1/4\ \mathrm{cov}_{AA}}{\sqrt{(V_{A(X)} + 1/4\ V_{AA(X)})(V_{A(Y)} + 1/4\ V_{AA(Y)})}}$$

2.) Dam components of variance and covariance

$$r_G = \frac{4\ \mathrm{cov}_D}{\sqrt{4\ \sigma^2_{D(X)}\ 4\ \sigma^2_{D(Y)}}} \qquad \text{(fours cancel)}$$

The genetic meaning is

$$r_G = \frac{\mathrm{cov}_A + \mathrm{cov}_D + \text{epistasis}}{\sqrt{(V_{A(X)} + V_{D(X)} + \ldots)(V_{A(Y)} + V_{D(Y)} + \ldots)}}$$

The genetic correlation obtained from these components has dominance and epistasis involved in its formulation.

3.) Dam + sire components

$$r_G = \frac{\mathrm{cov}_S + \mathrm{cov}_D}{\sqrt{\sigma^2_{S(X)} + \sigma^2_{D(X)}}\ \sqrt{\sigma^2_{S(Y)} + \sigma^2_{D(Y)}}}$$

This correlation also has dominance and epistasis involved in its estimation.

b. Environmental correlations

The objective is to obtain an estimate of the environmental correlation as free as possible of genetic variances and covariance.

1.)

$$r_E = \frac{\mathrm{cov}_W - 2\ \mathrm{cov}_S}{\sqrt{\sigma^2_{W(X)} - 2\ \sigma^2_{S(X)}}\ \sqrt{\sigma^2_{W(Y)} - 2\ \sigma^2_{S(Y)}}}$$

This estimate contains 3/4 cov_D and varying amounts of epistatic covariance in its numerator.

2.)

$$r_E = \frac{\mathrm{cov}_W - 2\ \mathrm{cov}_D}{\sqrt{\sigma^2_{W(X)} - 2\ \sigma^2_{D(X)}}\ \sqrt{\sigma^2_{W(Y)} - 2\ \sigma^2_{D(Y)}}}$$

This estimate contains 1/4 cov_D and smaller amounts of epistatic covariance than in 1.) above.

3.)

$$r_E = \frac{\mathrm{cov}_W + \mathrm{cov}_S - 3\ \mathrm{cov}_D}{\sqrt{\left(\sigma^2_{W(X)} + \sigma^2_{S(X)} - 3\ \sigma^2_{D(X)}\right)\left(\sigma^2_{W(Y)} + \sigma^2_{S(Y)} - 3\ \sigma^2_{D(Y)}\right)}}$$

This correlation has only small amounts of epistatic elements involved in its estimation.

c. Phenotypic correlation

$$r_P = \frac{\mathrm{cov}_W + \mathrm{cov}_S + \mathrm{cov}_D}{\sqrt{\sigma^2_{W(X)} + \sigma^2_{S(X)} + \sigma^2_{D(X)}}\ \sqrt{\sigma^2_{W(Y)} + \sigma^2_{S(Y)} + \sigma^2_{D(Y)}}}$$

5. Standard error of the genetic correlation (Mode and Robinson, 1959).

The variances of the mean squares and the mean cross products are obtained along with the covariances of the mean squares and the mean cross products in different combinations.

a. The variance of a mean square

$$\mathrm{var}\ (MS_g) = \frac{2\ MS_g^2}{f_g + 2}$$

where MS_g is the g^{th} mean square and f_g = the degrees of freedom of the g^{th} mean square.

The variances of the sire, dam, and full sib mean squares for each trait X and Y are calculated.

b. The variance of the mean cross products

$$\mathrm{var}\ (MCP_g) = \left[(MS_{g(x)})\ (MS_{g(y)}) + MCP_g^2\right] \Big/ f_g + 2$$

where MCP_g is the g^{th} mean cross product, $MS_{g(x)}$ is the g^{th} mean square for trait X and $MS_{g(y)}$ is the g^{th} mean square for trait Y.

c. The covariance of mean squares

$$\mathrm{cov}\ (MS_{g(x)},\ MS_{g(y)}) = \frac{2\ MCP_g^2}{f_g + 2}$$

d. The covariances of the mean square and mean cross product

$$\mathrm{cov}\ (MS_{g(x)},\ MCP_g) = \frac{2\ MS_{g(x)}\ MCP_g}{f_g + 2}$$

$$\text{cov}\ (MS_{g(y)},\ MCP_g) = \frac{2\ MS_{g(y)}\ MCP_g}{f_g + 2}$$

e. The variances of the analysis of variance and analysis of covariance components. These are obtained by summing the variances of the mean squares involved in estimating the component and dividing by the square of the coefficient of the component.

$$\text{var}\ (\sigma^2_{S(x)}) = \frac{\text{var}\ (MS_{S(x)}) + \text{var}\ (MS_{D(x)})}{k_3^2}$$

$$\text{var}\ (\sigma^2_{D(x)}) = \frac{\text{var}\ (MS_{D(x)}) + \text{var}\ (MS_{W(x)})}{k_1^2}$$

$$\text{var}\ (\sigma^2_{W(x)}) = \text{var}\ (MS_{W(x)})$$

The variances of the components for the trait Y are similarly obtained.

These formulas give the same results as the formulas on page 18.

f. The variance of the cross product components

$$\text{var}\ (\text{cov}_S) = \frac{\text{var}\ (MCP_S) + \text{var}\ (MCP_D)}{k_3^2}$$

$$\text{var}\ (\text{cov}_D) = \frac{\text{var}\ (MCP_D) + \text{var}\ (MCP_W)}{k_1^2}$$

$$\text{var}\ (\text{cov}_W) = \text{var}\ (MCP_W)$$

g. The covariances of the variance components

$$\text{cov}\ (\sigma^2_{S(x)},\ \sigma^2_{S(y)}) = \frac{\text{cov}\ (MS_{S(x)},\ MS_{S(y)}) + \text{cov}\ (MS_{D(x)},\ MS_{D(y)})}{k_3^2}$$

$$\text{cov}\ (\sigma^2_{D(x)},\ \sigma^2_{D(y)}) = \frac{\text{cov}\ (MS_{D(x)},\ MS_{D(y)}) + \text{cov}\ (MS_{W(x)}\ MS_{W(y)})}{k_1^2}$$

$$\text{cov}\ (\sigma^2_{W(x)},\ \sigma^2_{W(y)}) = \text{cov}\ (MS_{W(x)},\ MS_{W(y)})$$

h. The covariances of the analysis of variance and analysis of covariance components

$$\operatorname{cov}\,(\sigma^2_{S(x)},\ \operatorname{cov}_S) = \frac{\operatorname{cov}\,(MS_{S(x)},\ MCP_S) + \operatorname{cov}\,(MS_{D(x)}\ MCP_D)}{k_3^2}$$

$$\operatorname{cov}\,(\sigma^2_{D(x)},\ \operatorname{cov}_D) = \frac{\operatorname{cov}\,(MS_{D(x)},\ MCP_D) + \operatorname{cov}\,(MS_{W(x)}\ MCP_W)}{k_1^2}$$

$$\operatorname{cov}\,(\sigma^2_{W(x)},\ \operatorname{cov}_W) = \operatorname{cov}\,(MS_{W(x)},\ MCP_W)$$

The components of trait Y are similarly treated.

i. The general formula for the variance of the correlation coefficient, r

$$\operatorname{var}\,(r_g) \cong r^2 \left[\frac{\operatorname{var}\,(\operatorname{cov}_g)}{\operatorname{cov}_g^2} + \frac{\operatorname{var}\,(\sigma^2_{g(x)})}{4(\sigma^2_{g(x)})^2} + \frac{\operatorname{var}\,(\sigma^2_{g(y)})}{4(\sigma^2_{g(y)})^2} - \frac{\operatorname{cov}\,(\sigma^2_{g(x)},\ \operatorname{cov}_g)}{\sigma^2_{g(x)}\ \operatorname{cov}_g} - \frac{\operatorname{cov}\,(\sigma^2_{g(y)},\ \operatorname{cov}_g)}{\sigma^2_{g(y)},\ \operatorname{cov}_g} + \frac{\operatorname{cov}\,(\sigma^2_{g(x)},\ \sigma^2_{g(y)})}{2\sigma^2_{g(x)}\ \sigma^2_{g(y)}} \right]$$

The standard error would be the square root of the above quantity. For S.E. of genetic, environmental and phenotypic correlations of single pair and one-way layout designs see Scheinberg (1966).

6. Example

In Broad Breasted Bronze turkeys, seventeen single sire matings, four dams to a sire, were made and each mating produced three male progeny. At 24 weeks of age body weights and the shank length were measured. The mean body weight was 10,922 grams and mean shank length was 190.2 mm. What are the correlations between these two traits? Obtain the components of variance for each trait along with components of covariance.

Source	d.f.	Mean Squares and Mean Cross Products		
		Body weight MS	B.W. x S.L. MCP	Shank length MS
Sires	16	1,456,187	5,171	86.30
Dams	51	1,033,392	3,658	45.51
Sibs	136	810,551	3,105	36.47

Components of Variance and Covariance

Body Weight	B.W. x S.L.	Shank Length
$\sigma_S^2 = 35,233$	$\text{cov}_S = 126$	$\sigma_S^2 = 3.399$
$\sigma_D^2 = 74,280$	$\text{cov}_D = 184$	$\sigma_D^2 = 3.013$
$\sigma_W^2 = 810,551$	$\text{cov}_W = 3,105$	$\sigma_W^2 = 36.47$

a. Solve for genetic correlations

1.) Sire components

$$r_G = \frac{126}{\sqrt{35,233}\,\sqrt{3,399}} = 0.364$$

2.) Dam components

$$r_G = \frac{184}{\sqrt{74,280}\,\sqrt{3.013}} = 0.389$$

3.) Sire and dam components

$$r_G = \frac{126 + 184}{\sqrt{35,233 + 74,280}\,\sqrt{3.399 + 3.013}} = 0.369$$

b. Solve for environmental correlations

1.) Subtracting sire component

$$r_E = \frac{3,105 - 2\ (126)}{\sqrt{810,551 - 2(35,233)}\,\sqrt{36.47 - 2(3.399)}} = 0.608$$

2.) Subtracting dam's component

$$r_E = \frac{3,105 - 2\ (184)}{\sqrt{810,551 - 2\ (74,280)}\,\sqrt{36.47 - 2\ (3.013)}} = 0.609$$

3.) Adding sire's component minus 3 x dam's components

$$r_E = \frac{3,105 + 126 - 3(184)}{\sqrt{810,551 + 35,233 - 3(74,280)}\,\sqrt{36.47 + 3.399 - 3(3.013)}} = 0.695$$

c. Solve for phenotypic correlation

$$r_P = \frac{126 + 184 + 3,105}{\sqrt{35,233 + 74,280 + 810,551}\ \sqrt{3.399 + 3.013 + 36.47}} = 0.544$$

d. Standard error (worked out for the sire and the dam component genetic correlations).

1.) Variance of the mean squares and mean cross products

$$\text{var}\ (MS_{S(x)}) = \frac{2\ (1,456,187)^2}{16 + 2} = 2,356,089 \times 10^5$$

$$\text{var}\ (MCP_S) = \frac{(1,456,187)(86.30) + 5,171^2}{16 + 2} = 8,467,121$$

$$\text{var}\ (MS_{S(y)}) = \frac{2\ (86.30)^2}{16 + 2} = 827.52$$

etc.

Source	Body Weight	B.W. x S.L.	Shank Length
Sires	$2,356,089 \times 10^5$	8,467,121	827.52
Dams	$402,981 \times 10^5$	1,139,823	78.16
Sibs	$95,216 \times 10^5$	284,071	19.28

2.) Covariances of mean squares and cross products.

a.) Sires

$$\text{cov}\ (MS_{S(x)}, MS_{S(y)}) = \frac{(2)\ (5171)^2}{16 + 2} = 2,971,027$$

$$\text{cov}\ (MS_{S(x)}, MCP_S) = \frac{(2)\ (1,456,187)\ (5,171)}{16 + 2}$$

$$= 836,660 \times 10^3$$

$$\text{cov}\ (MS_{S(y)}, MCP_S) = \frac{(2)\ (86.30)\ (5,171)}{16 + 2} = 49,584$$

b.) Dams

$$\text{cov}\ (MS_{D(x)}, MS_{D(y)}) = \frac{2(3,658)^2}{51 + 2} = 504,942$$

$$\text{cov}\ (MS_{D(x)}, MCP_D) = \frac{(2)\ (1,033,392)\ (3,658)}{51 + 2}$$

$$= 142,647 \times 10^3$$

$$\text{cov}\ (MS_{D(y)}, MCP_D) = \frac{(2)\ (45.51)\ (3,658)}{51 + 2} = 6,282.10$$

c.) Sibs

$$\text{cov}\ (MS_{W(x)},\ MS_{W(y)}) = \frac{2\ (3105)^2}{136 + 2} = 139{,}725$$

$$\text{cov}\ (MS_{W(x)},\ MCP_W) = \frac{2\ (810{,}551)\ (3{,}105)}{136 + 2} = 36{,}474{,}795$$

$$\text{cov}\ (MS_{W(y)},\ MCP_W) = \frac{2\ (36.47)\ (3{,}105)}{136 + 2} = 1641.15$$

3.) Variances of the components of the analysis of variance and covariance

$k_1 = 3,\ k_3 = 12$

$$\text{var}\ (\sigma^2_{S(x)}) = \frac{2{,}356{,}089 \times 10^5 + 402{,}981 \times 10^5}{12^2} = 19{,}160 \times 10^5$$

$$\text{var}\ (\sigma^2_{D(x)}) = \frac{402{,}981 \times 10^5 + 95{,}216 \times 10^5}{3^2} = 55{,}355 \times 10^5$$

$$\text{var}\ (\sigma^2_{S(y)}) = \frac{827.52 + 78.16}{12^2} = 6.28944$$

$$\text{var}\ (\sigma^2_{D(y)}) = \frac{78.16 + 19.28}{3^2} = 10.8267$$

$$\text{var}\ (\text{cov}_S) = \frac{8{,}467{,}121 + 1{,}139{,}823}{12^2} = 66{,}715$$

$$\text{var}\ (\text{cov}_D) = \frac{1{,}139{,}823 + 284{,}071}{3^2} = 158{,}210$$

4.) Covariances of components

$$\text{cov}\ (\sigma^2_{S(x)},\ \sigma^2_{S(y)}) = \frac{2{,}971{,}027 + 504{,}942}{12^2} = 24{,}139$$

$$\text{cov}\ (\sigma^2_{D(x)},\ \sigma^2_{D(y)}) = \frac{504{,}942 + 139{,}725}{3^2} = 71{,}630$$

$$\text{cov}\ (\sigma^2_{S(x)},\ \text{cov}_S) = \frac{836{,}660 \times 10^3 + 142{,}647 \times 10^3}{12^2} = 6{,}800{,}743$$

$$\text{cov}\ (\sigma^2_{D(x)},\ \text{cov}_D) = \frac{142{,}647 \times 10^3 + 36{,}474{,}795}{3^2} = 19{,}902{,}422$$

$$\text{cov}\ (\sigma^2_{S(y)},\ \text{cov}_S) = \frac{49{,}584 + 6{,}282.10}{12^2} = 387.959$$

$$\text{cov}\ (\sigma^2_{D(x)},\ \text{cov}_D) = \frac{6{,}282.10 + 1{,}641.15}{3^2} = 880.361$$

5.) Variance of the genetic correlation

a.) Sire components

$r_G = 0.364$

$$\text{var}\ (r_G) \cong 0.364^2 \left[\frac{66{,}715}{126^2} + \frac{19{,}160 \times 10^5}{(4)35{,}233^2} + \frac{6.28944}{(4)3.399^2} - \frac{6{,}800{,}743}{(35{,}233)(126)} - \frac{387.959}{(126)\ (3.399)} + \frac{24{,}139}{2(35{,}233)\ (3.399)} \right] = 0.1325\ (2.3872) = 0.3163$$

$\sqrt{\text{var}(r_G)} = 0.562$

The correlation is 0.364 ± 0.562

b.) Dam's components

$r_G = 0.389$

$$\text{var}\ (r_G) \cong 0.389^2 \left[\frac{158{,}210}{184^2} + \frac{55{,}355 \times 10^5}{(4)74{,}280^2} + \frac{10.8267}{(4)3.013^2} - \frac{19{,}902{,}422}{74{,}280\ (184)} - \frac{880.333}{3.013\ (184)} + \frac{71{,}630}{2(74{,}280)\ (3.013)} \right] = 0.1513\ (2.3379)$$

$= 0.3537$

$\sqrt{\text{var}(r_G)} = 0.595$

The correlation is 0.389 ± 0.595

The standard errors are high because of the small numbers of sires and dams.

B. Factorial design

In plants a factorial design can be easily planned and genetic correlations obtained. Block and plot effects make it difficult to define environmental correlations because it would be expected that these environmental factors would change from one experiment to another.

1. Statistical model

The genetic variances are estimated as on page 34 for the factorial design. The analysis of covariance between the two traits X and Y is given for the following design: paternal and maternal plants are chosen at random from a non-inbred population. Each paternal plant is mated to every maternal plant and the full sib progeny of each mating planted one plot per mating to a replicate. There are several fixed replicates. The mean of the plots are used in the analysis:

Analysis of Covariance

Source	d.f.	MCP	EMCP
Replications	R - 1	MCP_R	-----------------------
Paternal	S - 1	MCP_S	$n_k cov_W + Rcov_{SD} + RDcov_S$
Maternal	D - 1	MCP_D	$n_k cov_W + Rcov_{SD} + RScov_D$
Paternal x maternal	(S - 1)(D - 1)	MCP_{SD}	$n_k cov_W + Rcov_{SD}$
Paternal - maternal Matings x replications	(SD-1)(R-1)	MCP_I	$n_k cov_W$

R = number of replications

S = number of paternal plants

D = number of maternal plants

$$n_k = \frac{1}{RSD} \sum_h \sum_i \sum_j \frac{1}{n_{hij}} \quad \text{(reciprocal of harmonic mean)}$$

2. Genetic model

In terms of the components of covariance

Source	cov_A	cov_D	cov_{AA}	cov_{AD}	cov_{DD}	cov_{AAA}	cov_E
cov_S	$\frac{1}{4}$	0	$\frac{1}{16}$	0	0	$\frac{1}{64}$	0
cov_D	$\frac{1}{4}$	0	$\frac{1}{16}$	0	0	$\frac{1}{64}$	0
cov_{SD}	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{32}$	0
cov_W	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{7}{8}$	$\frac{15}{16}$	$\frac{56}{64}$	1

3. Estimation of genetic correlation

a. Paternal component of variance and covariance

$$r_G = \frac{cov_{S(XY)}}{\sqrt{\sigma^2_{S(X)} \quad \sigma^2_{S(Y)}}}$$

b. Maternal components

$$r_G = \frac{cov_{D(XY)}}{\sqrt{\sigma^2_{D(X)} \quad \sigma^2_{D(Y)}}}$$

c. Maternal and paternal components combined

$$r_G = \frac{cov_S + cov_D}{\sqrt{\left[\sigma^2_{S(X)} + \sigma^2_{D(X)}\right] \left[\sigma^2_{S(Y)} + \sigma^2_{D(Y)}\right]}}$$

4. Computational formulas

With plot means, Z_{hij} will be the symbol designating the plot mean of the X trait on the h^{th} replicate of the mating of the i^{th} paternal plant and the j^{th} maternal plant. W_{hij} is similarly the plot mean of the Y trait.

Analysis of Covariance

Source	Sum of Cross Products	MCP
Correction term (C.T.)	$\frac{(Z_{...})(W_{...})}{RSD}$	
Replications	$\sum_h \frac{Z_{h..}W_{h..}}{SD}$ - C.T.	$SCP_R \Big/ R-1$
Paternal	$\sum_i \frac{Z_{.i.}W_{.i.}}{RD}$ - C.T.	$SCP_S \Big/ S-1$
Maternal	$\sum_j \frac{Z_{..j}W_{..j}}{RS}$ - C.T.	$SCP_D \Big/ D-1$
Paternal x Maternal	$\sum_i \sum_j \frac{Z_{.ij}W_{.ij}}{R} - \sum_j \frac{Z_{..j}W_{..j}}{RS} - \sum_i \frac{Z_{.i.}W_{.i.}}{RD}$ + C.T.	$SCP_{SD} \Big/ (S-1)(D-1)$
Paternal - Maternal Matings x Replications	$\sum_h \sum_i \sum_j Z_{hij} W_{hij} - \sum_i \sum_j \frac{Z_{.ij}W_{.ij}}{R} - \sum_h \frac{Z_{h..}W_{h..}}{SD}$ + C.T.	$SCP_I \Big/ (SD-1)(R-1)$

4. Estimating covariance components

$$\mathrm{cov}_S = \frac{\mathrm{MCP}_S - \mathrm{MCP}_{SD}}{RD}$$

$$\mathrm{cov}_D = \frac{\mathrm{MCP}_D - \mathrm{MCP}_{SD}}{RS}$$

5. Standard error of genetic correlation

The standard error is obtained using the formulas on pages 71-73. Because σ^2_S is estimated by subtracting the interaction mean square (MS_{SD}) from the paternal mean square (MS_S), when calculating var (σ^2_S), use the var (MS_{SD}) in the numerator rather than var (MS_D) as in the nested design. The same applies to var (cov_S). The coefficients for σ^2_S and cov_S will be RD and the coefficients for σ^2_D and cov_D will be RS.

C. Diallel crosses

Genetic correlations can be obtained from diallel crosses in a similar manner. See Griffing (1956) for a worked example.

II. Parent-offspring regression

The parent-offspring covariances can be used to estimate the genetic correlations. The same statistical procedures are used when covariances between the parent and offspring were obtained to estimate heritability.

A. Sire-offspring mean

This analysis follows that given on page 59. It is necessary to obtain four covariances between the sire and the mean of his offspring.

The general formula is

$$\Sigma xz = \Sigma XZ - \frac{(\Sigma X)(\Sigma Z)}{N}$$

$$\text{cov} = \frac{\Sigma xz}{N-1}$$

where N = number of sire-offspring pairs.

Consider traits as numbers 1 and 2.

$\text{cov}_{Z_2X_1}$ = covariance of trait Z_2 in offspring and trait X_1 in sire.

$\text{cov}_{Z_1X_2}$ = covariance of trait Z_1 in offspring and trait X_2 in sire.

$\text{cov}_{Z_1X_1}$ = covariance of trait Z_1 in offspring and trait X_1 in sire.

$\text{cov}_{Z_2X_2}$ = covariance of trait Z_2 in offspring and trait X_2 in sire.

The genetic correlation is obtained by:

1. Arithmetic method

a. $$r_G = \frac{\text{cov}_{Z_2X_1} + \text{cov}_{Z_1X_2}}{2\sqrt{\text{cov}_{Z_1X_1}\ \text{cov}_{Z_2X_2}}}$$

b. $$r_G = \frac{\mathrm{cov}_{Z_1X_2}}{\sqrt{\mathrm{cov}_{Z_1X_1}\ \mathrm{cov}_{Z_2X_2}}}$$

c. $$r_G = \frac{\mathrm{cov}_{Z_2X_1}}{\sqrt{\mathrm{cov}_{Z_1X_1}\ \mathrm{cov}_{Z_2X_2}}}$$

2. Geometric method

$$r_G = \sqrt{\frac{\mathrm{cov}_{Z_2X_1}\ \mathrm{cov}_{Z_1X_2}}{\mathrm{cov}_{Z_1X_1}\ \mathrm{cov}_{Z_2X_2}}}$$

Note that N - 1 is common to the numerator and denominator in all formulas. Thus, it is possible to use Σzx instead of the covariances, thereby eliminating an operation. Thus in 1a,

$$r_G = \frac{\Sigma z_2x_1 + \Sigma z_1x_2}{2\sqrt{\Sigma z_1x_1\ \Sigma z_2x_2}}$$

B. Intra-sire dam mean of offspring

The analysis of covariance for each trait is the same as on page 62.

Analysis of Covariance

Source	Sum of Cross Products	MCP
Sires	$\sum_i \frac{X_{i.}Z_{i.}}{n_i}$	----------
Dams/Sires	$\sum_i \sum_j X_{ij}Z_{ij} - \sum_i \frac{X_{i.}Z_{i.}}{n_i}$	$\mathrm{SCP}/\mathrm{D-S}$

The four covariances as obtained previously in sire-mean of offspring are calculated: $\mathrm{cov}_{Z_2X_1}$, $\mathrm{cov}_{Z_1X_2}$, $\mathrm{cov}_{Z_1X_1}$, $\mathrm{cov}_{Z_2X_2}$.

The genetic correlations are derived as before in sire-mean of offspring. Note that the sum of cross products (SCP) can be used instead of covariances (or Mean Cross Products) in these formulas because the degrees of freedom cancel.

C. Standard error of the genetic correlation (Reeve, 1955 and Robertson, 1959).

$$\text{S.E. } (r_G) \cong \frac{1 - r_G^2}{\sqrt{2}} \sqrt{\frac{\text{S.E. } (h_1^2) \quad \text{S.E. } (h_2^2)}{h_1^2 \; h_2^2}}$$

The standard errors of the heritabilities are estimated from the regression analysis (see pages 60, 64).

D. Example

Fifteen single pair matings were made with Coturnix quail. The 4-week body weights and body temperatures were measured on the parents and the offspring. The covariances of the female offspring and the dam's observation were calculated.

Trait 1 = body weight
Trait 2 = body temperature

Means

	Body weight (grams)	Body temperature (°C)
Dams	90.80	40.21
Female progeny	93.02	40.40

$\text{cov}_{Z_1X_1} = 23.16$ $\qquad$ $\text{cov}_{Z_1X_2} = 0.3033$

$\text{cov}_{Z_2X_2} = 0.0507$ $\qquad$ $\text{cov}_{Z_2X_2} = 0.1453$

h_1^2 (body weight) = (2) 0.298 = 0.596 ± 0.529

h_2^2 (body temperature) = (2) 0.125 = 0.250 ± 0.550

1. Arithmetic method

a. $$r_G = \frac{0.3033 + 0.1453}{2\sqrt{(0.0507)(23.16)}} = \frac{0.4486}{2\sqrt{1.1742}} = 0.207$$

b. $$r_G = \frac{0.3033}{\sqrt{1.1742}} = 0.280$$

c. $$r_G = \frac{0.1453}{\sqrt{1.1742}} = 0.134$$

If there are large differences between the variances of the dam's observations and the offspring's records, then a correction has to be made to b and c above (Dickerson, 1960).

2. Geometric method

$$r_G = \sqrt{\frac{(0.3033)(0.1453)}{(0.0507)(23.16)}} = 0.194$$

Van Vleck and Henderson (1961) have run a genetic simulation problem and have compared the use of these methods. They found formula 1a is preferable to 1b and 1c. Situations where only one cross covariance would be available that would necessitate using 1b or 1c are probably rare.

3. Standard errors (for arithmetic method)

$$\text{S.E. } (r_G) \cong \frac{1 - 0.414^2}{\sqrt{2}} \sqrt{\frac{(0.529)(0.550)}{(0.596)(0.250)}} = 0.819$$

$$r_G = 0.414 \pm 0.819$$

SELECTION INDEX

I. Introduction

A selection index is used when the breeder simultaneously selects for several characters. They are also used when selecting two or more traits and information is available on the individual and its relatives. When selecting line crosses it is possible to utilize indexes (Henderson, 1963). This section illustrates how to construct a selection index based on the economic weights and genetic parameters when two or more traits are measured on an individual.

A. Required information:

1. The genetic and phenotypic variances: V_A and V_P for every trait considered in the selection index.
2. The genetic and phenotypic covariances: cov_A and cov_P between each pair of traits. Occasionally heritability and genetic correlations are given for the different traits. Then these particular estimates have to be solved to obtain the estimates required above (1 and 2). Because of rounding errors, significant digits are lost in this process, and therefore correlation coefficients are not used in this section.
3. The economic weights ($a_1, a_2, \ldots a_k$) for each trait. These economic weights are based on the value in terms of the price data and net profit. See Hogsett and Nordskog (1958) for an example of economic weighting in chickens.

The aggregate genotypic value of the index is:

$$H = a_1 G_1 + a_2 G_2 + \ldots a_k G_k$$

where the a's refer to the relative economic values, the G's are the genotypic values of the trait, and i = 1, 2, . . . k traits.

B. Set up normal simultaneous equations: Normal simultaneous equations are used to obtain the b_i's which are the partial regression coefficients needed to construct a selection index, I.

$$I = b_1X_1 + b_2X_2 + \ldots + b_kX_k$$

where $X_1, X_2, \ldots, X_k$ are the phenotypic values of the traits 1, 2 . . ., k; and $b_1, b_2, \ldots, b_k$ are the coefficients for each trait.

The normal simultaneous equations for k traits are given below:

$$V_{P(X_1)}b_1 + \mathrm{cov}_{P(X_1X_2)}b_2 + \cdots + \mathrm{cov}_{P(X_1X_k)}b_k = V_{A(X_1)}a_1 + \mathrm{cov}_{A(X_1X_2)}a_2 + \cdots + \mathrm{cov}_{A(X_1X_k)}a_k$$

$$\mathrm{cov}_{P(X_2X_1)}b_1 + V_{P(X_2)}b_2 + \cdots + \mathrm{cov}_{P(X_2X_k)}b_k = \mathrm{cov}_{A(X_2X_1)}a_1 + V_{A(X_2)}a_2 + \cdots \mathrm{cov}_{A(X_2X_k)}a_k$$

$$\mathrm{cov}_{P(X_kX_1)}b_1 + \mathrm{cov}_{P(X_kX_2)}b_2 + \cdots + V_{P(X_k)}b_k = \mathrm{cov}_{A(X_kX_1)}a_1 + \mathrm{cov}_{A(X_kX_2)}a_2 + \cdots + V_{A(X_k)}a_k$$

where $V_{P(X_i)}$ = phenotypic variance of i^{th} trait, $V_{A(X_i)}$ = additive genetic variance of the i^{th} trait, $\mathrm{cov}_{P(X_iX_j)}$ = phenotypic covariance of i^{th} and j^{th} trait, a_i = economic weight of the i^{th} trait, b_i = partial regression coefficient of i^{th} trait. $\mathrm{cov}_{A(X_iX_j)}$ = additive genetic covariance.

These equations are solved for the b's. Two methods will be given in this section, one involving two traits and another with k numbers of traits utilizing matrix algebra.

II. Two traits

The construction of a selection index involving two traits is given below.

A. Computational formulas

1. Set up the normal simultaneous equations

$$V_{P(X_1)}b_1 + \mathrm{cov}_{P(X_1X_2)}b_2 = V_{A(X_1)}a_1 + \mathrm{cov}_{A(X_1X_2)}a_2 \qquad \text{(i)}$$

$$\mathrm{cov}_{P(X_1X_2)}b_1 + V_{P(X_2)}b_2 = \mathrm{cov}_{A(X_1X_2)}a_1 + V_{A(X_2)}a_2 \qquad \text{(ii)}$$

2. Multiply the a's times the estimates of genetic parameters.

3. Divide equation (i) by $\mathrm{cov}_{P(X_1X_2)}$ and obtain equation (iii).

4. Divide equation (ii) by $V_{P(X_2)}$ and obtain equation (iv).

Note: operations 3 and 4 could also be carried out by dividing each equation by the coefficients of the b_1's.

5. Subtract equation (iii) - (iv) and obtain (v).
6. Solve for b_1 in (v).
7. Substitute b_1 in equation (iii) or (iv) and solve for b_2.
8. Construct selection index $I = b_1 X_1 + b_2 X_2$
9. To simplify index, divide right hand side by b_2 or b_1.

B. Example. Two traits in swine, feed conversion and eye muscle area, were measured in a British testing program (slightly modified data from the Animal Breeding Organization, Edinburgh, Scotland).

1. Required Estimates

    a. Economic Weights

        1.) Feed Conversion. A 0.1 increase in feed conversion (expressed as the ratio of body weight gain to the amount of feed consumed) corresponds to an increase of 15.5 pounds of feed. If the cost of the feed is 360 pence per 112 pounds, then the loss is

$$\frac{15.5}{112} \times 360 = -50 \text{ pence for 0.1 increase}$$

$$a_1 = -50$$

        2.) Eye Muscle Area. In the range of weights the eye muscle area of the last sib would have an influence on the value of the carcass of 12 pence for each square centimeter.

a_2 = 12 pence per increase in one square centimeter

    b. Estimates of Biological Parameters

        1.) Feed Conversion (X_1)

$$V_{A(X_1)} = 0.03125$$

$$V_{P(X_1)} = 0.0625$$

$$h^2_{(X_1)} = 0.50$$

2.) Eye Muscle Area (X_2)

$V_{A(X_2)} = 4.05$

$V_{P(X_2)} = 9.0$

$h^2_{(X_2)} = 0.45$

3.) Covariances (X_1X_2)

$cov_{A(X_1X_2)} = -0.1125$

$cov_{P(X_1X_2)} = -0.481$

$r_{G(X_1X_2)} = -0.356$

$r_{P(X_1X_2)} = -0.65$

2. Normal Equations Solution

a. Set Up Equations

$0.0625\, b_1 - 0.481\, b_2 = 0.03125\ (-50) - 0.1125\ (12)$ (i)

$-0.481\, b_1 + 9.0\, b_2 = -0.1125\ (-50) + 4.05\ (12)$ (ii)

b. The right hand portions of the equations are multiplied and summed

$0.0625\, b_1 - 0.481\, b_2 = -2.9125$ (i)

$-0.481\, b_1 + 9.0\, b_2 = 54.225000$ (ii)

c. Divide (i) by -0.481

$-0.129938\, b_1 + b_2 = 6.055093$ (iii)

d. Divide (ii) by 9.0

$-0.053444\, b_1 + b_2 = 6.025000$ (iv)

e. Subtract (iii) - (iv)

$-0.076494\, b_1 = 0.030093$

$b = -0.393403$

f. Substitute b_1 in (iv) (or iii) and solve for b_2

$$-0.053444\ (-0.393403) + b_2 = 6.025000$$

$$b_2 = 6.003974$$

g. Construct selection index

$$I = -0.393403\ X_1 + 6.003974\ X_2$$

h. Simplifying the index (divide by 0.393403)

$$I = -X_1 + 15.261640\ X_2$$

III. More than two traits (matrix algebra)

A. General formulas

The normal simultaneous equations used previously can be represented by matrices. In this work it is essential to carry as many places as possible because of rounding errors (see Searle 1966, pgs. 102-104).

Phenotypic matrix $\qquad$ b vector

$$\begin{bmatrix} V_{P(X_1)} & cov_{P(X_1X_2)} & \cdots\cdots & cov_{P(X_1X_k)} \\ cov_{P(X_2X_1)} & V_{P(X_2)} & \cdots\cdots & cov_{P(X_2X_k)} \\ \vdots & \vdots & & \vdots \\ cov_{P(X_kX_1)} & cov_{P(X_kX_2)} & \cdots\cdots & V_{P(X_k)} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ \vdots \\ b_k \end{bmatrix} =$$

Genotypic matrix $\qquad$ a vector

$$\begin{bmatrix} V_{A(X_1)} & cov_{A(X_1X_2)} & \cdots\cdots & cov_{A(X_1X_k)} \\ cov_{A(X_2X_1)} & V_{A(X_2)} & \cdots\cdots & cov_{A(X_2X_k)} \\ \vdots & \vdots & & \vdots \\ cov_{A(X_kX_1)} & cov_{A(X_kX_2)} & \cdots\cdots & V_{A(X_k)} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_k \end{bmatrix}$$

and the selection index can be represented as

$$[I] = [b_1\ b_2\ \cdots\cdots\ b_k] \begin{bmatrix} X_1 \\ X_2 \\ \vdots \\ X_k \end{bmatrix}$$

$$I = b_1X_1 + b_2X_2 + \ldots b_kX_k$$

These matrices can be symbolized as $P\,\underline{b} = G\,\underline{a}$

where P is the variance-covariance matrix of phenotypic values, G is the variance-covariance matrix of genotypic values, $\underline{b}$ is the vector of partial regression coefficients of the X's in the index,

$$I = \underline{b}\,X$$

and $\underline{a}$ is the vector of relative economic values.

The matrices each have i rows and j columns and the elements can be designated by P_{ij} or g_{ij} for the phenotypic and genotypic matrices respectively. In regression problems, the matrices are symmetrical so the number of rows = the number of columns = k. The regression coefficients and economic values vectors can be considered as one column matrices.

B. Augmented matrix solution $P\,\underline{b} = G\,\underline{a}$

The genotypic matrix G is multiplied by the economic weights vector $\underline{a}$.

$$G\underline{a} = \begin{bmatrix} g_{11} & g_{12} & \cdots & g_{1j} \\ g_{21} & g_{22} & \cdots & g_{2j} \\ \vdots & \vdots & & \vdots \\ g_{i1} & g_{i2} & \cdots & g_{kk} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_k \end{bmatrix}$$

$$\begin{array}{l} g_{11}\,a_1 + g_{12}\,a_2 + \cdots + g_{1j}\,a_k = d_1 \\ g_{21}\,a_1 + g_{22}\,a_2 + \cdots + g_{2j}\,a_k = d_2 \\ \vdots \\ g_{i1}\,a_1 + g_{i2}\,a_2 + \cdots + g_{kk}\,a_k = d_k \end{array}$$

This vector, $\underline{d}$, is the product of $G\,\underline{a}$. Then $P\,\underline{b} = \underline{d}$.

The abbreviated Doolittle method can be used to solve this equation for the b's. The reader is referred to Dwyer, 1951; Anderson and Bancroft, 1952 (pp. 191-200); Steel and Torrie, 1960 (pp. 289-296); Searle, 1966, or other suitable books.

The notation and instructions are similar to that of the example given in Steel and Torrie (1960), page 290.

Set up a table

Instruction		P Matrix		Ga Matrix	Check
		X_1	$X_2 \cdot \cdot \cdot X_k$	y	c
1	X_1	p_{11}	$p_{12} \cdot \cdot \cdot p_{1k}$	y_1	c_1
	X_2		$p_{22} \cdot \cdot \cdot p_{2k}$	y_2	c_2
	$\vdots$		$\vdots$	$\vdots$	$\vdots$
	X_k		p_{kk}	y_k	c_k
2	A_{1j}	A_{11}	$A_{12} \cdot \cdot \cdot A_{1k}$	A_{1y}	A_{1c}
	B_{1j}	1	$B_{12} \cdot \cdot \cdot B_{1k}$	B_{1y}	B_{1c}
3	A_{2j}		$A_{22} \cdot \cdot \cdot A_{2k}$	A_{2y}	A_{2c}
	B_{2j}		$1 \cdot \cdot \cdot B_{2k}$	B_{2y}	B_{2c}

Instruction

1) Enter the values of the P and Ga matrices. The check column consists of the sum of the observation on that line, e.g. $c_2 = p_{21} + p_{22} + \cdot \cdot \cdot p_{2k} + y_2$ where $p_{21} = p_{12}$. The full matrix should be used even though it is not all filled in.

2) Copy first line of instruction 1. Divide each element by p_{11}. $B_{12} = A_{12}/A_{11} = p_{12}/p_{11}$. The subscripts y and c refer to location in the instructions; y is the Ga matrix and c is the check. The check is obtained by $B_{1c} = A_{1c}/A_{11}$ and is checked against the sum of the elements in the line.

3) The A entry for the j^{th} column is obtained where $j = 2, 3, \cdot \cdot \cdot k, y, c$.

$$A_{2j} = p_{2j} - A_{12} B_{1j} \text{ or } p_{2j} - A_{1j} B_{12}$$

The B entry is computed by dividing each A by A_{22}

$$B_{22} = A_{22}/A_{22} = 1$$

$$B_{2k} = A_{2k}/A_{22}$$

This procedure continues for each additional trait. The number of columns in the P matrix should equal the number of traits and the number of instructions is k + 1. The last instruction then has $B_{kk} = A_{kk}/A_{kk} = 1$

4) Obtain the partial regression coefficient b's.

$$b_k = B_{ky}$$

and the b's are computed by working backwards, so

$$b_{k-1} = B_{(k-1)y} - (B_{(k-1)k}\ b_k)$$

$$b_{k-2} = B_{(k-2)y} - (B_{(k-2)(k-1)}\ b_{(k-1)} + B_{(k-2)k}\ b_k)$$

etc.

$$b_1 = B_{1y} - (B_{12}\ b_2 + B_{13}\ b_3 + \ldots + B_{1k}\ b_k)$$

If the inverse of the phenotypic matrix, P^{-1}, is desired, as in the next section, then the following steps are followed.

5) A c matrix is obtained with c_{11}, c_{12} . . . etc.

$$c_{kk} = 1/A_{kk}$$

$$c_{(k-1)k} = - B_{(k-1)k}\ c_{kk}$$

$$c_{(k-2)k} = - B_{(k-2)(k-1)}\ c_{(k-1)k} - B_{(k-2)k}\ c_{kk}$$

$$c_{(k-3)k} = - B_{(k-3)(k-2)}\ c_{(k-2)k} - B_{(k-3)(k-1)}\ c_{(k-1)k} - B_{(k-3)k}\ c_{kk}$$

etc.

where k = 4

$$c_{(k-1)(k-1)} = 1/A_{(k-1)(k-1)} - B_{(k-3)(k-2)}\ c_{(k-3)(k-2)} - B_{(k-2)(k-1)}\ c_{(k-2)(k-1)} - B_{(k-1)k}\ c_{(k-1)k}$$

Note $c_{ij} = c_{ji}$

C. Inverting the phenotypic matrix.

The b's can be computed by $\underline{b} = P^{-1}\,G\,\underline{a}$

The phenotypic matrix is inverted as given previously and this inverse is multiplied by the genotypic matrix.

$$\begin{bmatrix} c_{11} & c_{12} & \cdots & c_{1j} \\ c_{21} & c_{22} & \cdots & c_{2j} \\ \vdots & \vdots & & \vdots \\ c_{i1} & c_{i2} & \cdots & c_{kk} \end{bmatrix} \begin{bmatrix} g_{11} & g_{12} & \cdots & g_{1j} \\ g_{21} & g_{22} & \cdots & g_{2j} \\ \vdots & \vdots & & \\ g_{i1} & g_{i2} & \cdots & g_{kk} \end{bmatrix}$$

Multiply the elements of the i^{th} row of the inverted phenotypic matrix, C, by the corresponding elements in the k^{th} column of the genotypic matrix and sum. Thus, to obtain the d elements of the new matrix, D

$$d_{11} = c_{11}\,g_{11} + c_{12}\,g_{21} + c_{13}\,g_{31} + \cdots + c_{1j}\,g_{i1}$$

$$d_{21} = c_{21}\,g_{11} + c_{22}\,g_{21} + c_{23}\,g_{31} + \cdots + c_{2j}\,g_{i1}$$

$$d_{12} = c_{11}\,g_{12} + c_{12}\,g_{22} + c_{13}\,g_{32} + \cdots + c_{1j}\,g_{i2}, \text{ etc.}$$

The economic value vector is multiplied with matrix D. $\underline{b} = D\,\underline{a}$

$$\underline{b} = \begin{bmatrix} d_{11} & d_{12} & \cdots & d_{1j} \\ d_{21} & d_{22} & \cdots & d_{2j} \\ \vdots & \vdots & & \vdots \\ d_{i1} & d_{i2} & \cdots & d_{kk} \end{bmatrix} \qquad \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_k \end{bmatrix}$$

Multiply and obtain the vector $\underline{b}$ with elements b_i.

$$\begin{bmatrix} d_{11}\,a_1 + d_{12}\,a_2 + \cdots + d_{ij}\,a_k \\ d_{21}\,a_1 + d_{22}\,a_2 + \cdots + d_{2j}\,a_k \\ \vdots \qquad \vdots \qquad \vdots \\ d_{i1}\,a_1 + d_{i2}\,a_2 + \cdots + d_{kk}\,a_k \end{bmatrix} \begin{matrix} = \\ = \\ \\ = \end{matrix} \begin{bmatrix} b_1 \\ b_2 \\ \vdots \\ b_k \end{bmatrix}$$

The augmented matrix method is simpler to do by hand calculator than the inverse method but the inverse method has the advantage that the economic value vector multiplication can be left to the last. Thus, any change in the economic values requires only that the new economic value vector $\underline{a}$ be multiplied with the D matrix to obtain the new b's for a new index.

D. Variance of the index

$$\sigma_I^2 = \underline{b}' \; P \; \underline{b}$$

where $\underline{b}'$ is the transverse of $\underline{b}$ vector.

The transverse of $\underline{b}$ vector is

$$\underline{b}' = [b_1 \; b_2 \; b_3 \; \cdots\cdots\cdots \; b_k]$$

E. Example. Same as given previously using two traits, feed conversion and eye muscle area in swine.

1. Augmented matrix method

a. Set up matrices $P \; \underline{b} = G \; \underline{a}$

$$\begin{array}{ccccc} P & \underline{b} & & G & \underline{a} \\ \begin{bmatrix} 0.0625 & -0.481 \\ -0.481 & 9.0 \end{bmatrix} & \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} & = & \begin{bmatrix} 0.03125 & -0.1125 \\ -0.1125 & 4.05 \end{bmatrix} & \begin{bmatrix} -50 \\ 12 \end{bmatrix} \end{array}$$

b. Multiply the genotypic matrix times the economic values vector.

$$\begin{bmatrix} 0.03125 \quad (-50) + -0.1125 \quad (12) \\ -0.1125 \quad (-50) \quad + \quad 4.05 \quad (12) \end{bmatrix} = \begin{bmatrix} -2.912500 \\ 54.225000 \end{bmatrix}$$

The augmented matrix is

$$Pb = \underline{d}$$

$$\begin{bmatrix} 0.0675 & -0.481 \\ -0.481 & 9.0 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} -2.912500 \\ 54.225000 \end{bmatrix}$$

c. Set up abbreviated Doolittle table and solve for b's.

		P matrix		$\underline{d}$	Check
Instruction		X_1	X_2	y	c
1	X_1	0.0625	-0.481	-2.912500	-3.331000
	X_2		9.0	54.225000	62.744000
2	A_{ij}	0.0625	-0.481	-29.12500	-3.331000
	B_{ij}	1	-7.696000	-46.600000	-53.296000
3	A_{2j}		5.298224	31.810400	37.108624
	B_{2j}		1	6.003974	7.003974

Instruction 1. Insert augmented matrix values

$c_1 = 0.0625 - 0.481 - 2.912500 = -3.331000$

$c_2 = -0.481 + 9.0 + 54.225000 = 62.744000$

Instruction 2. Line A_{ij} is copied from line X_1

$B_{11} = 0.0625/0.0625 = 1$

$B_{12} = -0.481/0.0625 = -7.696000$

$B_{13} = -2.912500/0.0625 = -46.600000$

$B_{1c} = -3.331000/0.0625 = -53.296000$

which checks with

$1 - 7.696000 - 46.600000 = -53.296000$

Instruction 3.

$A_{22} = 9.0 - (-0.481)(-7.696000) = 5.298224$

$A_{2g} = 54.225000 - (-0.481)(-46.600000) = 31.810400$

$A_{2c} = 62.744000 - (-0.481)(-53.296000) = 37.108624$

which checks with

$5.298224 + 31.810400 = 37.108624$

$B_{22} = 5.298224/5.298224 = 1$

$B_{2y} = 31.810400/5.298224 = 6.003974$

$B_{2c} = 37.108624/5.298224 = 7.003974$

which checks with

$1 + 6.003974 = 7.003974$

Obtaining the regression coefficients, b's

$b_2 = B_{2y} = 6.003974$

$b_1 = B_{1y} - B_{12}b_2 = -46.600000 - (-7.696000)(6.003974) = -0.393415$

which differs from the previous estimates in the fifth place because of rounding errors.

2. Inverse matrix method

a. Obtain the inverse of the phenotypic matrix. The elements (c's) are:

$c_{22} = 1/A_{22} = 1/5.298224 = 0.188743$

$c_{21} = c_{12} = -B_{12}\ c_{22} = -\ (7.696000)(0.188743) = 1.452566$

$c_{11} = 1/A_{11} - B_{12}\ c_{12} = 1/0.0625 - (-7.696000)(1.452566) = 27.178948$

Thus

$$P^{-1} = \begin{bmatrix} 27.178948 & 1.452566 \\ 1.452566 & 0.188743 \end{bmatrix}$$

b. Multiply the inverse phenotypic matrix times the genotypic matrix

$$\underset{p-1}{\begin{bmatrix} 27.178948 & 1.452566 \\ 1.452566 & 0.188743 \end{bmatrix}} \qquad \underset{G}{\begin{bmatrix} 0.03125 & -0.1125 \\ -0.1125 & 4.05 \end{bmatrix}}$$

The elements (d's) of the D matrix are

$d_{11} = (27.178948)(0.03125) + (1.452566)(-0.1125) = 0.685928$

$d_{21} = (1.452566)(0.03125) + (0.188743)(-0.1125) = 0.0241591$

$$d_{12} = (27.178948)(-0.1125) + (1.452566)(4.05) = 2.8252606$$

$$d_{22} = (1.452566)(-0.1125) + (0.188743)(4.05) = 0.6009954$$

c. The D matrix is multiplied by the economic values vector, a, and the b vector obtained.

$$\underline{b} = \overset{D}{\begin{bmatrix} 0.685928 & 2.825261 \\ 0.0241591 & 0.600995 \end{bmatrix}} \quad \overset{\underline{a}}{\begin{bmatrix} -50 \\ 12 \end{bmatrix}}$$

$$b_1 = (0.685928)(-50) + (2.825261)(12) = -0.389080$$

$$b_2 = (0.0241591)(-50) + (0.600995)(12) = 6.003985$$

INFORMATION FROM RELATIVES

It is possible to estimate the breeding value of an individual from relatives' information.

I. Assumptions

A. No sex linkage.
B. The mated animals are unrelated (however, see Jardine, 1958, pg. 505).
C. Additive genetic variance only is considered.
D. No herd effects (however, see Skjervold and Odegard, 1959, pg. 347).
E. No common environmental effects, maternal, etc. (see Jardine, 1958, pg. 501).

II. Several records per individual

The heritability increases when several records are compiled on an animal. Examples would be successive shearings of sheep, lactations of a cow, number in successive litters of savine. The mean of these records is then used as the phenotypic observation on that animal.

Because it is a mean, heritability increases in accordance with the formula

$$h_m^2 = h_1^2 \quad \frac{m}{1 + (m-1)R}$$

where m = number of records on an individual; h_m^2 = heritability when m records are taken on an individual; h_1^2 = heritability of single records; R = repeatability.

The formula $\frac{m}{1 + (m-1)R}$ is given in table 1 for different numbers of records and repeatabilities.

III. Estimation of breeding value

Breeding value of individual = $b_1 (X_I - \bar{x}_P) + b_2 (X_D - \bar{x}_P) + b_3 (X_S - \bar{x}_P) + b_4 (X_{MD} - \bar{x}_P) + b_5 (X_{SD} - \bar{x}_P) + b_6 (\bar{x}_{HS} - \bar{x}_P) + b_7 (\bar{x}_{FS} - \bar{x}_P) + b_8 (\bar{x}_o - \bar{x}_P)$.

where the symbols I = individual, D = dam, S = sire, MD = maternal granddam, SD = paternal granddam, HS = half sibs, FS = full sibs, O = offspring, $\bar{x}_P$ = phenotypic mean of the population. The breeding value of the individual is expressed as the deviation from its population mean.

The regression coefficients (b's) are given below for several common situations

A. Ancestor records only

1. Dam or sire record

$$b_2 = 0.5\ h_D^2 \quad \text{or} \quad b_3 = 0.5\ h_S^2$$

2. Dam's record and maternal granddam

$$b_2 = \frac{h^2_D\ (4 - h^2_{MD})}{2\ (4 - h^2_D\ h^2_{MD})}$$

$$b_4 = \frac{2\ h^2_{MD}\ (1 - h^2_D)}{2\ (4 - h^2_D\ h^2_{MD})}$$

Example. In dairy cattle the maternal granddam of a young bull had four records of milk production averaging 12,000 pounds. Her population mean was 9,500 pounds. The dam had two records averaging 11,500 and the mean of her population was 9,200. With heritability of milk production 0.3 and repeatability 0.4, what is the estimated breeding value of the bull?

a. Obtain heritabilities of multiple records using table 1.

$$h_2 = 0.3\ (1.43) = 0.429$$

$$h_4 = 0.3\ (1.82) = 0.546$$

b. Solve for b_2

$$b_2 = \frac{0.429\ (4 - 0.546)}{2\ [(4 - (0.429)(0.546)]} = \frac{1.482}{7.532} = 0.20$$

c. Solve for b_4

$$b_4 = \frac{2\ (0.546)(1 - 0.429)}{7.532} = \frac{0.623}{7.532} = 0.083$$

d. Using general estimation equation, solve for breeding value.

$$\text{B.V.} = b_2\ (X_D - \bar{x}_P) + b_4\ (X_{MD} - \bar{x}_P) = 0.20\ (11{,}500 - 9{,}200)$$

$$+ 0.083\ (12{,}000 - 9{,}500) = 460 + 207.5 = 667.5$$

The estimated breeding value of the bull is 667.5 lbs. of milk expressed as the deviation from his population mean.

3. Dam + maternal granddam + paternal granddam

b_2 and b_4 are the same as in B above $\quad b_5 = 0.25\ h^2_{SD}$

B. Ancestors and Individuals

1. Individual alone

$$b_1 = h^2_I$$

2. Individual + dam's or sire's record

$$b_1 = \frac{h_I^2 (4 - h_D^2)}{4 - h_I^2 h_D^2}$$

$$b_2 = \frac{2 h_D^2 (1 - h_I^2)}{4 - h_I^2 h_D^2}$$

If b_2 is used instead of b_3 then h_S^2 is substituted for h_D^2 in formula for b_2.

For further combinations see Skjervold and Odegard (1959).

C. Ancestors and sibs

The record of the individual is not included in the mean of the sibs.

$$N = \frac{nd}{1 + (nd-1)\, t}$$

where n = number of full sibs per family.
d = number of dams mated to a sire.
t = intraclass correlation which in the case where n = 1 is $0.25\ h^2$.

1. Dam + paternal half sibs

$$b_2 = 0.5\ h_D^2$$

$$b_6 = 0.25\ h_{HS}^2\ N$$

2. Sire + paternal half sibs

$$b_3 = \frac{h_S^2 (4 - h_{HS}^2\ N)}{2\ (4 - h_S^2 h_{HS}^2\ N)}$$

$$b_6 = \frac{h_{HS}^2\ N\ (1 - h_S^2)}{4 - h_S^2 h_{HS}^2\ N}$$

3. Individual + dam + paternal half sibs

$$b_1 = \frac{h_I^2 (16 - 4\ h_D^2 + h_{HS}^2\ N)}{16 - 4\ h_D^4 + h_{HS}^4\ N}$$

$$b_2 = \frac{8\ h_D^2\ (1 - h_I^2)}{16 - 4\ h_D^4 + h_{HS}^4\ N}$$

$$b_6 = \frac{4\ h_{HS}^2\ N\ (1 - h_I^2)}{16 - 4\ h_D^4 + h_{HS}^4\ N}$$

For further combinations see Young (1961).

D. Sibs

It is assumed that only one record is available on each animal.

1. Individual's record included

Full and half sib information is given along with the individual's record.

$$b_1 = \frac{h^2}{2 - h^2}$$

$$b_6 = \frac{4\ nd\ (1 - h^2)\ h^2}{[4 + (n - 2)\ h^2]\ [4 + (n\ (d + 1) - 2)]\ h^2}$$

$$b_7 = \frac{h^2}{2 - h^2} \cdot \frac{2\ n\ (1 - h^2)}{4 + (n - 2)\ h^2}$$

2. Individual's record is not included. An example would be the selection of males in poultry.

$$b_6 = \frac{2\ nd\ h^2\ (2 - h^2)}{\{4 + (n - 2)\ h^2\}\ \{4 + [n\ (d + 1) - 2]\ h^2\}}$$

$$b_7 = \frac{n\ h^2}{4 + (n - 2)\ h^2}$$

when n varies among full sib families, replace nd by the number of individuals in the sire family. Compute the partial regression coefficients separately for each full sib family and determine the coefficients for each sire family using nd.

See Osborne (1957 a,b)

E. Progeny

N is as defined before. When there is a mixture of full and half sibs

$$t = \frac{n\ (d + 1) - 2}{4\ (dn - 1)}$$

1. Progeny only

$$b_8 = 0.5\ h_O^2\ N$$

2. Individual + progeny

$$b_1 = \frac{2\ dn\ (\ 1 - h^2)\ h^2}{[1 + (n - 1)\ 2\ h^2 + n\ (d - 1)\ h^2] - dnh^4}$$

$$b_8 = (1 - \tfrac{1}{2}\ b_1)\ h^2$$

where n is equal for each full sib family. See Jardine (1958) for coefficients when n is unequal.

3. Dam + paternal half sibs + half sib progeny. Example would be determining the breeding value of a dairy bull.

$$b_2 = \frac{8\ h_D^2\ (4 - h_O^2\ N)}{64 - h_O^2\ N\ (4\ h_D^2 + h_{HS}^2\ N)}$$

$$b_6 = \frac{4\ h_{HS}^2\ N\ (4 - h_O^2\ N)}{64 - h_O^2\ N\ (4\ h_D^2 + h_{HS}^2\ N)}$$

$$b_8 = \frac{2\ h_O^2\ N\ (16 - 4\ h_D^2 + h_{HS}^2\ N)}{64 - h_O^2\ N\ (4\ h_D^2 + h_{HS}^2\ N)}$$

For further combinations see Jardine (1958) and Young (1961).

TABLES

Table 1. The equation, $\frac{m}{1 + (m - 1) R}$, solved for 1 - 6 records per individual with different repeatabilities.

Number of records (m)	Repeatability (R)								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	1.82	1.67	1.54	1.43	1.33	1.25	1.18	1.11	1.05
3	2.50	2.14	1.88	1.67	1.50	1.36	1.25	1.15	1.07
4	2.86	2.50	2.11	1.82	1.60	1.43	1.29	1.18	1.08
5	3.33	2.78	2.27	1.92	1.67	1.47	1.32	1.19	1.09
6	3.75	3.00	2.40	2.00	1.71	1.50	1.33	1.20	1.09

Table 2. Standardized selection differential when population size is less than 400.*

No. Selected	Number in Population 2	3	4	5	6	7	8	9	10	No. Selected
1	0.564	0.846	1.029	1.163	1.267	1.352	1.424	1.485	1.539	1
2		0.423	0.663	0.829	0.954	1.055	1.138	1.209	1.270	2
3			0.343	0.553	0.704	0.821	0.916	0.996	1.065	3
4				0.291	0.477	0.616	0.725	0.816	0.893	4
5					0.253	0.422	0.550	0.653	0.739	5
6						0.225	0.379	0.498	0.595	6
7							0.203	0.345	0.457	7
8								0.186	0.318	8
9									0.171	9

No. Selected	Number in Population 11	12	13	14	15	16	17	18	19	No. Selected
1	1.586	1.629	1.668	1.703	1.736	1.766	1.794	1.820	1.844	1
2	1.324	1.372	1.416	1.456	1.492	1.525	1.556	1.585	1.612	2
3	1.126	1.179	1.227	1.271	1.311	1.347	1.381	1.412	1.441	3
4	0.960	1.019	1.071	1.119	1.162	1.201	1.237	1.271	1.302	4
5	0.813	0.877	0.935	0.986	1.032	1.075	1.114	1.150	1.183	5
6	0.677	0.748	0.811	0.866	0.916	0.962	1.003	1.042	1.077	6
7	0.548	0.627	0.695	0.755	0.809	0.858	0.902	0.943	0.981	7
8	0.422	0.509	0.584	0.650	0.708	0.760	0.808	0.851	0.891	8
9	0.294	0.393	0.476	0.548	0.611	0.667	0.718	0.764	0.807	9
10	0.159	0.274	0.368	0.447	0.516	0.577	0.632	0.681	0.726	10
11		0.148	0.257	0.347	0.422	0.489	0.547	0.600	0.648	11
12			0.139	0.243	0.328	0.400	0.464	0.521	0.572	12
13				0.131	0.230	0.311	0.381	0.442	0.497	13
14					0.124	0.218	0.296	0.363	0.423	14
15						0.118	0.208	0.282	0.347	15
16							0.112	0.198	0.270	16
17								0.107	0.190	17
18									0.102	18

*Estimates of the standardized selection differential for numbers between the rows or columns of this table may be obtained by a linear approximation. The figures in this table were obtained by averaging data given by Harter (1961).

Table 2, continued

	20	21	22	23	24	25	26	27	28	29	
1	1.867	1.889	1.910	1.929	1.948	1.965	1.982	1.998	2.014	2.029	1
2	1.638	1.661	1.684	1.705	1.726	1.745	1.763	1.781	1.798	1.814	2
3	1.469	1.494	1.519	1.542	1.563	1.584	1.604	1.623	1.641	1.658	3
4	1.332	1.359	1.385	1.410	1.433	1.455	1.476	1.496	1.515	1.533	4
5	1.214	1.244	1.271	1.297	1.322	1.345	1.367	1.388	1.408	1.427	5
6	1.110	1.141	1.170	1.198	1.224	1.248	1.271	1.293	1.314	1.334	6
7	1.016	1.049	1.079	1.108	1.135	1.161	1.185	1.208	1.230	1.251	7
8	0.928	0.963	0.995	1.025	1.054	1.081	1.106	1.130	1.153	1.175	8
9	0.846	0.882	0.916	0.948	0.978	1.006	1.032	1.058	1.082	1.104	9
10	0.767	0.806	0.842	0.875	0.906	0.936	0.963	0.990	1.015	1.038	10
11	0.692	0.733	0.770	0.805	0.838	0.869	0.898	0.925	0.951	0.976	11
12	0.619	0.662	0.701	0.738	0.772	0.805	0.835	0.863	0.890	0.916	12
13	0.547	0.592	0.634	0.673	0.709	0.743	0.774	0.804	0.832	0.859	13
14	0.476	0.524	0.569	0.609	0.647	0.683	0.716	0.747	0.776	0.804	14
15	0.405	0.457	0.504	0.547	0.587	0.624	0.658	0.691	0.721	0.750	15
16	0.333	0.389	0.439	0.485	0.527	0.566	0.602	0.636	0.668	0.698	16
17	0.259	0.320	0.374	0.423	0.467	0.508	0.547	0.582	0.615	0.647	17
18	0.182	0.249	0.308	0.360	0.408	0.451	0.492	0.529	0.564	0.596	18
19	0.098	0.175	0.240	0.297	0.348	0.394	0.437	0.476	0.512	0.546	19
20		0.094	0.168	0.231	0.287	0.336	0.381	0.423	0.461	0.497	20
21			0.091	0.162	0.223	0.277	0.325	0.370	0.410	0.448	21
22				0.088	0.157	0.216	0.268	0.315	0.358	0.398	22
23					0.085	0.152	0.209	0.260	0.306	0.348	23
24						0.082	0.147	0.203	0.252	0.297	24
25							0.079	0.142	0.197	0.245	25
26								0.077	0.138	0.191	26
27									0.075	0.134	27
28										0.072	28

Table 2, continued

	30	31	32	33	34	35	36	37	38	39	
1	2.043	2.056	2.070	2.082	2.095	2.107	2.118	2.129	2.140	2.151	1
2	1.829	1.844	1.858	1.872	1.886	1.898	1.911	1.923	1.935	1.946	2
3	1.674	1.690	1.706	1.720	1.734	1.748	1.761	1.774	1.787	1.799	3
4	1.550	1.567	1.583	1.599	1.614	1.628	1.642	1.656	1.669	1.681	4
5	1.446	1.463	1.480	1.496	1.512	1.527	1.542	1.556	1.570	1.583	5
6	1.354	1.372	1.390	1.407	1.423	1.439	1.454	1.469	1.483	1.497	6
7	1.271	1.290	1.309	1.327	1.344	1.360	1.376	1.391	1.406	1.420	7
8	1.196	1.216	1.235	1.254	1.271	1.288	1.305	1.321	1.336	1.351	8
9	1.126	1.147	1.167	1.186	1.204	1.222	1.239	1.255	1.271	1.287	9
10	1.061	1.083	1.103	1.123	1.142	1.160	1.178	1.195	1.211	1.227	10
11	0.999	1.022	1.043	1.064	1.083	1.102	1.120	1.138	1.155	1.171	11
12	0.941	0.964	0.986	1.007	1.028	1.047	1.066	1.084	1.101	1.118	12
13	0.884	0.908	0.931	0.953	0.974	0.994	1.014	1.032	1.050	1.068	13
14	0.830	0.855	0.879	0.902	0.923	0.944	0.964	0.983	1.002	1.020	14
15	0.777	0.803	0.828	0.852	0.874	0.895	0.916	0.936	0.955	0.973	15
16	0.726	0.753	0.779	0.803	0.826	0.848	0.870	0.890	0.910	0.929	16
17	0.676	0.704	0.731	0.756	0.780	0.803	0.825	0.846	0.866	0.885	17
18	0.627	0.656	0.683	0.710	0.734	0.758	0.781	0.802	0.823	0.843	18
19	0.579	0.609	0.637	0.664	0.690	0.714	0.738	0.760	0.782	0.802	19
20	0.530	0.562	0.592	0.620	0.646	0.672	0.696	0.719	0.741	0.762	20
21	0.483	0.515	0.546	0.576	0.603	0.629	0.654	0.678	0.701	0.723	21
22	0.435	0.469	0.501	0.532	0.560	0.588	0.613	0.638	0.662	0.684	22
23	0.387	0.423	0.457	0.488	0.518	0.546	0.573	0.599	0.623	0.646	23
24	0.338	0.376	0.412	0.445	0.476	0.505	0.533	0.559	0.584	0.608	24
25	0.289	0.329	0.367	0.401	0.434	0.464	0.493	0.520	0.546	0.571	25
26	0.239	0.281	0.321	0.357	0.391	0.423	0.453	0.481	0.508	0.534	26
27	0.186	0.232	0.274	0.313	0.348	0.382	0.413	0.443	0.470	0.497	27
28	0.131	0.181	0.226	0.267	0.305	0.340	0.373	0.404	0.433	0.460	28
29	0.070	0.127	0.176	0.221	0.261	0.298	0.332	0.364	0.395	0.423	29
30		0.069	0.124	0.172	0.215	0.255	0.291	0.325	0.356	0.386	30
31			0.067	0.121	0.168	0.210	0.249	0.284	0.317	0.349	31
32				0.065	0.118	0.164	0.205	0.243	0.278	0.311	32
33					0.063	0.115	0.160	0.201	0.238	0.272	33
34						0.062	0.112	0.157	0.196	0.233	34
35							0.061	0.110	0.153	0.192	35
36								0.059	0.107	0.150	36
37									0.058	0.105	37
38										0.057	38

Table 2, continued

	40	41	42	43	44	45	46	47	48	49	
1	2.161	2.171	2.180	2.190	2.199	2.208	2.216	2.225	2.233	2.241	1
2	1.957	1.968	1.978	1.988	1.998	2.008	2.017	2.026	2.035	2.044	2
3	1.810	1.822	1.833	1.843	1.854	1.864	1.874	1.883	1.893	1.902	3
4	1.694	1.706	1.717	1.728	1.739	1.750	1.760	1.770	1.780	1.790	4
5	1.596	1.608	1.620	1.632	1.643	1.654	1.665	1.675	1.686	1.696	5
6	1.510	1.523	1.536	1.548	1.560	1.571	1.582	1.593	1.604	1.614	6
7	1.434	1.447	1.460	1.473	1.485	1.497	1.509	1.520	1.531	1.542	7
8	1.365	1.379	1.392	1.405	1.418	1.430	1.442	1.454	1.465	1.476	8
9	1.301	1.316	1.330	1.343	1.356	1.369	1.381	1.393	1.405	1.416	9
10	1.242	1.257	1.271	1.285	1.299	1.312	1.324	1.337	1.349	1.360	10
11	1.187	1.202	1.217	1.231	1.245	1.258	1.271	1.284	1.296	1.308	11
12	1.134	1.150	1.165	1.180	1.194	1.208	1.221	1.234	1.247	1.259	12
13	1.084	1.101	1.116	1.131	1.146	1.160	1.174	1.187	1.200	1.213	13
14	1.037	1.053	1.069	1.085	1.100	1.114	1.129	1.142	1.156	1.169	14
15	0.991	1.008	1.024	1.040	1.056	1.071	1.085	1.099	1.113	1.126	15
16	0.947	0.964	0.981	0.998	1.013	1.029	1.044	1.058	1.072	1.086	16
17	0.904	0.922	0.939	0.956	0.972	0.988	1.003	1.018	1.032	1.046	17
18	0.862	0.881	0.899	0.916	0.933	0.949	0.964	0.980	0.994	1.008	18
19	0.822	0.841	0.859	0.877	0.894	0.911	0.927	0.942	0.957	0.972	19
20	0.782	0.802	0.821	0.839	0.857	0.873	0.890	0.906	0.921	0.936	20
21	0.744	0.764	0.783	0.802	0.820	0.837	0.854	0.870	0.886	0.901	21
22	0.706	0.726	0.746	0.765	0.784	0.802	0.819	0.836	0.852	0.867	22
23	0.668	0.689	0.710	0.730	0.749	0.767	0.784	0.801	0.818	0.834	23
24	0.631	0.653	0.674	0.694	0.714	0.733	0.751	0.768	0.785	0.801	24
25	0.595	0.617	0.639	0.660	0.680	0.699	0.717	0.735	0.753	0.769	25
26	0.558	0.582	0.604	0.625	0.646	0.665	0.684	0.703	0.721	0.738	26
27	0.522	0.546	0.569	0.591	0.612	0.633	0.652	0.671	0.689	0.707	27
28	0.486	0.511	0.535	0.557	0.579	0.600	0.620	0.639	0.658	0.676	28
29	0.450	0.476	0.500	0.524	0.546	0.568	0.588	0.608	0.627	0.646	29
30	0.414	0.441	0.466	0.490	0.513	0.535	0.557	0.577	0.597	0.615	30
31	0.378	0.405	0.432	0.457	0.481	0.503	0.525	0.546	0.566	0.586	31
32	0.341	0.370	0.397	0.423	0.448	0.471	0.494	0.515	0.536	0.556	32
33	0.304	0.334	0.363	0.389	0.415	0.439	0.462	0.485	0.506	0.526	33
34	0.267	0.298	0.328	0.355	0.382	0.407	0.431	0.454	0.476	0.497	34
35	0.228	0.261	0.292	0.321	0.349	0.375	0.400	0.423	0.446	0.467	35
36	0.188	0.223	0.256	0.286	0.315	0.342	0.368	0.392	0.416	0.438	36
37	0.147	0.184	0.219	0.251	0.281	0.309	0.336	0.361	0.385	0.408	37
38	0.103	0.144	0.181	0.215	0.246	0.276	0.304	0.330	0.355	0.379	38
39	0.055	0.101	0.141	0.177	0.211	0.242	0.271	0.298	0.324	0.349	39
40		0.054	0.099	0.138	0.174	0.207	0.237	0.266	0.293	0.319	40
41			0.053	0.097	0.136	0.171	0.203	0.233	0.261	0.288	41
42				0.052	0.095	0.133	0.168	0.199	0.229	0.257	42
43					0.051	0.093	0.131	0.165	0.196	0.225	43
44						0.050	0.092	0.128	0.162	0.193	44
45							0.049	0.090	0.126	0.159	45
46								0.048	0.088	0.124	46
47									0.048	0.087	47
48										0.047	48

Table 2, continued

	50	55	60	65	70	75	80	85	90	95	
1	2.249	2.286	2.319	2.350	2.377	2.403	2.427	2.449	2.470	2.489	1
2	2.052	2.092	2.127	2.160	2.189	2.217	2.242	2.266	2.288	2.308	2
3	1.911	1.953	1.990	2.024	2.055	2.084	2.111	2.135	2.159	2.180	3
4	1.799	1.843	1.882	1.918	1.950	1.980	2.008	2.033	2.057	2.080	4
5	1.705	1.751	1.792	1.829	1.862	1.893	1.922	1.948	1.973	1.996	5
6	1.624	1.671	1.713	1.752	1.786	1.818	1.848	1.875	1.901	1.925	6
7	1.552	1.601	1.644	1.683	1.719	1.752	1.782	1.811	1.837	1.861	7
8	1.487	1.537	1.582	1.622	1.659	1.693	1.724	1.752	1.779	1.804	8
9	1.427	1.479	1.525	1.566	1.604	1.638	1.670	1.700	1.727	1.753	9
10	1.372	1.425	1.472	1.514	1.553	1.588	1.621	1.651	1.679	1.705	10
11	1.320	1.374	1.423	1.466	1.506	1.542	1.575	1.606	1.634	1.661	11
12	1.271	1.327	1.376	1.421	1.461	1.498	1.532	1.563	1.593	1.620	12
13	1.225	1.282	1.333	1.378	1.419	1.457	1.492	1.524	1.553	1.581	13
14	1.181	1.240	1.291	1.338	1.380	1.418	1.453	1.486	1.516	1.544	14
15	1.139	1.199	1.252	1.299	1.342	1.381	1.417	1.450	1.481	1.510	15
16	1.099	1.160	1.214	1.262	1.306	1.346	1.382	1.416	1.447	1.476	16
17	1.060	1.122	1.177	1.227	1.271	1.312	1.349	1.383	1.415	1.445	17
18	1.022	1.086	1.142	1.193	1.238	1.279	1.317	1.352	1.384	1.414	18
19	0.986	1.051	1.109	1.160	1.206	1.248	1.286	1.322	1.354	1.385	19
20	0.951	1.017	1.076	1.128	1.175	1.217	1.257	1.292	1.326	1.357	20
21	0.916	0.984	1.044	1.097	1.145	1.188	1.228	1.264	1.298	1.329	21
22	0.882	0.952	1.013	1.067	1.116	1.160	1.200	1.237	1.271	1.303	22
23	0.849	0.920	0.983	1.038	1.087	1.132	1.173	1.210	1.245	1.277	23
24	0.817	0.890	0.953	1.009	1.059	1.105	1.147	1.185	1.220	1.253	24
25	0.786	0.860	0.924	0.981	1.032	1.079	1.121	1.160	1.195	1.228	25
26	0.754	0.830	0.896	0.954	1.006	1.053	1.096	1.135	1.171	1.205	26
27	0.724	0.801	0.868	0.927	0.980	1.028	1.071	1.111	1.148	1.182	27
28	0.693	0.772	0.841	0.901	0.955	1.003	1.047	1.088	1.125	1.159	28
29	0.663	0.744	0.814	0.875	0.930	0.979	1.024	1.065	1.103	1.138	29
30	0.634	0.716	0.788	0.850	0.906	0.956	1.001	1.042	1.081	1.116	30
31	0.604	0.689	0.761	0.825	0.882	0.932	0.978	1.020	1.059	1.095	31
32	0.575	0.662	0.736	0.801	0.858	0.910	0.956	0.999	1.038	1.074	32
33	0.546	0.635	0.710	0.776	0.835	0.887	0.934	0.978	1.017	1.054	33
34	0.517	0.608	0.685	0.752	0.812	0.865	0.913	0.957	0.997	1.034	34
35	0.488	0.581	0.660	0.729	0.789	0.843	0.892	0.936	0.977	1.015	35
36	0.459	0.555	0.635	0.705	0.767	0.821	0.871	0.916	0.957	0.995	36
37	0.430	0.528	0.611	0.682	0.744	0.800	0.850	0.896	0.938	0.976	37
38	0.401	0.502	0.586	0.659	0.722	0.779	0.830	0.876	0.919	0.958	38
39	0.372	0.476	0.562	0.636	0.701	0.758	0.810	0.857	0.900	0.939	39
40	0.343	0.450	0.538	0.613	0.679	0.738	0.790	0.838	0.881	0.921	40
41	0.313	0.423	0.514	0.591	0.658	0.717	0.770	0.819	0.863	0.903	41
42	0.283	0.397	0.490	0.568	0.637	0.697	0.751	0.800	0.844	0.885	42
43	0.253	0.370	0.466	0.546	0.615	0.677	0.732	0.781	0.826	0.868	43
44	0.221	0.344	0.441	0.524	0.594	0.657	0.713	0.763	0.809	0.851	44
45	0.189	0.317	0.417	0.501	0.574	0.637	0.694	0.745	0.791	0.833	45
46	0.156	0.289	0.393	0.479	0.553	0.617	0.675	0.726	0.773	0.816	46
47	0.122	0.262	0.369	0.457	0.532	0.598	0.656	0.709	0.756	0.800	47

Table 2, continued

	50	55	60	65	70	75	80	85	90	95	
48	0.085	0.233	0.344	0.434	0.511	0.578	0.637	0.691	0.739	0.783	48
49	0.046	0.205	0.319	0.412	0.491	0.559	0.619	0.673	0.722	0.767	49
50		0.175	0.294	0.390	0.470	0.539	0.601	0.655	0.705	0.750	50
51		0.145	0.269	0.367	0.449	0.520	0.582	0.638	0.688	0.734	51
52		0.113	0.243	0.345	0.429	0.501	0.564	0.620	0.671	0.718	52
53		0.079	0.217	0.322	0.408	0.481	0.546	0.603	0.655	0.702	53
54		0.042	0.190	0.299	0.387	0.462	0.528	0.586	0.638	0.686	54
55			0.163	0.275	0.366	0.443	0.509	0.569	0.622	0.670	55
56			0.134	0.252	0.345	0.423	0.491	0.551	0.605	0.654	56
57			0.105	0.228	0.324	0.404	0.473	0.534	0.589	0.638	57
58			0.073	0.203	0.302	0.384	0.455	0.517	0.573	0.623	58
59			0.039	0.178	0.281	0.365	0.437	0.500	0.557	0.607	59
60				0.152	0.259	0.345	0.419	0.483	0.540	0.592	60
61				0.126	0.237	0.325	0.401	0.466	0.524	0.576	61
62				0.098	0.214	0.305	0.382	0.449	0.508	0.561	62
63				0.069	0.191	0.285	0.364	0.432	0.492	0.546	63
64				0.037	0.167	0.265	0.346	0.415	0.476	0.530	64
65					0.143	0.244	0.327	0.398	0.460	0.515	65
66					0.118	0.223	0.308	0.380	0.444	0.500	66
67					0.092	0.202	0.289	0.363	0.427	0.485	67
68					0.064	0.180	0.270	0.346	0.411	0.469	68
69					0.034	0.158	0.251	0.328	0.395	0.454	69
70						0.135	0.232	0.311	0.379	0.439	70
71						0.112	0.212	0.293	0.362	0.423	71
72						0.087	0.192	0.275	0.346	0.408	72
73						0.061	0.171	0.257	0.330	0.393	73
74						0.032	0.150	0.239	0.313	0.377	74
75							0.128	0.220	0.296	0.362	75
76							0.106	0.201	0.279	0.346	76
77							0.082	0.182	0.262	0.331	77
78							0.057	0.162	0.245	0.315	78
79							0.031	0.142	0.228	0.299	79
80								0.122	0.210	0.283	80
81								0.100	0.192	0.267	81
82								0.078	0.174	0.251	82
83								0.055	0.155	0.234	83
84								0.029	0.136	0.218	84
85									0.116	0.201	85
86									0.096	0.183	86
87									0.074	0.166	87
88									0.052	0.148	88
89									0.028	0.130	89
90										0.111	90
91										0.091	91
92										0.071	92
93										0.050	93
94										0.026	94

Table 2, continued

	100	125	150	175	200	225	250	300	350	400	
1	2.508	2.586	2.649	2.701	2.746	2.785	2.819	2.878	2.927	2.968	1
2	2.328	2.411	2.478	2.533	2.580	2.621	2.657	2.718	2.769	2.813	2
3	2.201	2.288	2.357	2.414	2.463	2.506	2.543	2.607	2.660	2.705	3
4	2.101	2.191	2.263	2.322	2.372	2.416	2.455	2.520	2.574	2.621	4
5	2.018	2.111	2.185	2.246	2.297	2.342	2.382	2.449	2.504	2.552	5
6	1.947	2.043	2.118	2.181	2.233	2.279	2.320	2.388	2.445	2.493	6
7	1.884	1.982	2.060	2.123	2.177	2.224	2.265	2.335	2.393	2.442	7
8	1.828	1.928	2.007	2.072	2.127	2.175	2.217	2.288	2.346	2.396	8
9	1.777	1.879	1.960	2.026	2.082	2.130	2.173	2.245	2.304	2.355	9
10	1.730	1.834	1.916	1.983	2.040	2.089	2.132	2.206	2.266	2.317	10
11	1.686	1.792	1.876	1.944	2.002	2.052	2.095	2.170	2.231	2.283	11
12	1.645	1.753	1.838	1.907	1.966	2.017	2.061	2.136	2.198	2.250	12
13	1.607	1.717	1.803	1.873	1.932	1.984	2.029	2.105	2.167	2.220	13
14	1.571	1.682	1.770	1.841	1.901	1.953	1.998	2.075	2.139	2.192	14
15	1.536	1.650	1.738	1.810	1.871	1.924	1.970	2.048	2.112	2.166	15
16	1.504	1.619	1.708	1.781	1.843	1.896	1.943	2.021	2.086	2.141	16
17	1.472	1.589	1.680	1.754	1.816	1.870	1.917	1.996	2.061	2.117	17
18	1.442	1.560	1.652	1.727	1.790	1.845	1.892	1.972	2.038	2.094	18
19	1.413	1.533	1.626	1.702	1.766	1.821	1.869	1.950	2.016	2.072	19
20	1.386	1.507	1.601	1.678	1.742	1.798	1.846	1.928	1.995	2.051	20
21	1.359	1.482	1.577	1.655	1.720	1.775	1.824	1.907	1.974	2.031	21
22	1.333	1.457	1.554	1.632	1.698	1.754	1.803	1.886	1.955	2.012	22
23	1.308	1.434	1.531	1.610	1.677	1.733	1.783	1.867	1.936	1.993	23
24	1.283	1.411	1.509	1.589	1.656	1.714	1.764	1.848	1.917	1.976	24
25	1.259	1.388	1.488	1.569	1.636	1.694	1.745	1.830	1.900	1.958	25
26	1.236	1.367	1.467	1.549	1.617	1.675	1.726	1.812	1.882	1.942	26
27	1.214	1.346	1.447	1.530	1.598	1.657	1.709	1.795	1.866	1.925	27
28	1.192	1.325	1.428	1.511	1.580	1.640	1.691	1.778	1.850	1.910	28
29	1.170	1.305	1.409	1.493	1.563	1.622	1.675	1.762	1.834	1.894	29
30	1.149	1.286	1.390	1.475	1.545	1.606	1.658	1.746	1.819	1.879	30
31	1.128	1.266	1.372	1.457	1.529	1.589	1.642	1.731	1.804	1.865	31
32	1.108	1.248	1.354	1.440	1.512	1.573	1.627	1.716	1.789	1.851	32
33	1.088	1.229	1.337	1.424	1.496	1.558	1.612	1.702	1.775	1.837	33
34	1.069	1.211	1.320	1.408	1.480	1.543	1.597	1.687	1.761	1.823	34
35	1.050	1.194	1.304	1.392	1.465	1.528	1.582	1.673	1.748	1.810	35
36	1.031	1.176	1.287	1.376	1.450	1.513	1.568	1.660	1.734	1.797	36
37	1.012	1.159	1.271	1.361	1.435	1.499	1.554	1.646	1.722	1.785	37
38	0.994	1.143	1.255	1.346	1.421	1.485	1.540	1.633	1.709	1.772	38
39	0.976	1.126	1.240	1.331	1.407	1.471	1.527	1.620	1.697	1.760	39
40	0.958	1.110	1.225	1.317	1.393	1.458	1.514	1.608	1.684	1.749	40
41	0.941	1.094	1.210	1.302	1.379	1.444	1.501	1.596	1.672	1.737	41
42	0.923	1.078	1.195	1.288	1.366	1.431	1.488	1.583	1.661	1.726	42
43	0.906	1.063	1.181	1.275	1.352	1.418	1.476	1.572	1.649	1.714	43
44	0.889	1.047	1.166	1.261	1.339	1.406	1.464	1.560	1.638	1.704	44
45	0.873	1.032	1.152	1.248	1.327	1.393	1.452	1.548	1.627	1.693	45
46	0.856	1.018	1.138	1.235	1.314	1.381	1.440	1.537	1.616	1.682	46
47	0.840	1.003	1.125	1.222	1.301	1.369	1.428	1.526	1.605	1.672	47
48	0.824	0.988	1.111	1.209	1.289	1.357	1.417	1.515	1.595	1.662	48
49	0.808	0.974	1.098	1.196	1.277	1.346	1.405	1.504	1.584	1.651	49

Table 2, continued

	100	125	150	175	200	225	250	300	350	400	
50	0.792	0.960	1.085	1.184	1.265	1.334	1.394	1.494	1.574	1.642	50
51	0.776	0.946	1.072	1.171	1.253	1.323	1.383	1.483	1.564	1.632	51
52	0.760	0.932	1.059	1.159	1.242	1.312	1.372	1.473	1.554	1.622	52
53	0.745	0.918	1.046	1.147	1.230	1.301	1.362	1.463	1.544	1.613	53
54	0.729	0.904	1.034	1.135	1.219	1.290	1.351	1.453	1.535	1.603	54
55	0.714	0.891	1.021	1.124	1.208	1.279	1.341	1.443	1.525	1.594	55
56	0.699	0.877	1.009	1.112	1.197	1.268	1.330	1.433	1.516	1.585	56
57	0.684	0.864	0.997	1.101	1.186	1.258	1.320	1.423	1.507	1.576	57
58	0.669	0.851	0.985	1.089	1.175	1.248	1.310	1.414	1.497	1.567	58
59	0.654	0.838	0.973	1.078	1.165	1.237	1.300	1.404	1.488	1.558	59
60	0.639	0.825	0.961	1.067	1.154	1.227	1.290	1.395	1.479	1.550	60
61	0.624	0.812	0.949	1.056	1.144	1.217	1.281	1.386	1.471	1.541	61
62	0.609	0.799	0.937	1.045	1.133	1.207	1.271	1.377	1.462	1.533	62
63	0.594	0.787	0.926	1.034	1.123	1.197	1.262	1.368	1.453	1.525	63
64	0.580	0.774	0.914	1.024	1.113	1.188	1.252	1.359	1.445	1.516	64
65	0.565	0.761	0.903	1.013	1.103	1.178	1.243	1.350	1.436	1.508	65
66	0.551	0.749	0.892	1.003	1.093	1.169	1.234	1.342	1.428	1.500	66
67	0.536	0.737	0.881	0.992	1.083	1.159	1.225	1.333	1.420	1.492	67
68	0.521	0.724	0.869	0.982	1.073	1.150	1.216	1.324	1.412	1.484	68
69	0.507	0.712	0.858	0.972	1.064	1.141	1.207	1.316	1.404	1.477	69
70	0.492	0.700	0.847	0.961	1.054	1.131	1.198	1.308	1.396	1.469	70
71	0.478	0.688	0.837	0.951	1.044	1.122	1.189	1.299	1.388	1.461	71
72	0.463	0.676	0.826	0.941	1.035	1.113	1.181	1.291	1.380	1.454	72
73	0.449	0.664	0.815	0.931	1.026	1.104	1.172	1.283	1.372	1.446	73
74	0.434	0.652	0.804	0.922	1.016	1.095	1.163	1.275	1.365	1.439	74
75	0.420	0.640	0.794	0.912	1.007	1.087	1.155	1.267	1.357	1.432	75
76	0.405	0.628	0.783	0.902	0.998	1.078	1.147	1.259	1.350	1.425	76
77	0.391	0.616	0.773	0.892	0.989	1.069	1.138	1.252	1.342	1.417	77
78	0.376	0.604	0.762	0.883	0.980	1.061	1.130	1.244	1.335	1.410	78
79	0.361	0.592	0.752	0.873	0.971	1.052	1.122	1.236	1.327	1.403	79
80	0.346	0.581	0.742	0.864	0.962	1.044	1.114	1.228	1.320	1.396	80
81	0.332	0.569	0.731	0.854	0.953	1.035	1.106	1.221	1.313	1.389	81
82	0.317	0.557	0.721	0.845	0.944	1.027	1.098	1.213	1.306	1.382	82
83	0.302	0.546	0.711	0.836	0.936	1.019	1.090	1.206	1.299	1.376	83
84	0.286	0.534	0.701	0.826	0.927	1.011	1.082	1.199	1.292	1.369	84
85	0.271	0.522	0.691	0.817	0.918	1.002	1.074	1.191	1.285	1.362	85
86	0.256	0.511	0.680	0.808	0.910	0.994	1.066	1.184	1.278	1.356	86
87	0.240	0.499	0.670	0.799	0.901	0.986	1.059	1.177	1.271	1.349	87
88	0.224	0.487	0.660	0.790	0.893	0.978	1.051	1.170	1.264	1.343	88
89	0.208	0.476	0.650	0.781	0.884	0.970	1.043	1.163	1.258	1.336	89
90	0.192	0.464	0.640	0.772	0.876	0.962	1.036	1.156	1.251	1.330	90
91	0.176	0.453	0.631	0.763	0.868	0.955	1.028	1.149	1.244	1.323	91
92	0.159	0.441	0.621	0.754	0.860	0.947	1.021	1.142	1.238	1.317	92
93	0.142	0.429	0.611	0.745	0.851	0.939	1.013	1.135	1.231	1.311	93
94	0.124	0.418	0.601	0.736	0.843	0.931	1.006	1.128	1.225	1.305	94
95	0.106	0.406	0.591	0.727	0.835	0.924	0.999	1.121	1.218	1.298	95
96	0.088	0.394	0.581	0.719	0.827	0.916	0.991	1.114	1.212	1.292	96
97	0.068	0.383	0.572	0.710	0.819	0.908	0.984	1.108	1.205	1.286	97
98	0.048	0.371	0.562	0.701	0.811	0.901	0.977	1.101	1.199	1.280	98
99	0.025	0.359	0.552	0.692	0.803	0.893	0.970	1.094	1.193	1.274	99

Table 2, continued

	100	125	150	175	200	225	250	300	350	400	
100		0.347	0.542	0.684	0.795	0.886	0.963	1.088	1.187	1.268	100
101		0.335	0.533	0.675	0.787	0.878	0.956	1.081	1.180	1.262	101
102		0.323	0.523	0.667	0.779	0.871	0.949	1.075	1.174	1.256	102
103		0.311	0.513	0.658	0.771	0.864	0.942	1.068	1.168	1.251	103
104		0.299	0.504	0.649	0.763	0.856	0.935	1.062	1.162	1.245	104
105		0.287	0.494	0.641	0.755	0.849	0.928	1.055	1.156	1.239	105
106		0.275	0.484	0.632	0.748	0.842	0.921	1.049	1.150	1.233	106
107		0.263	0.474	0.624	0.740	0.834	0.914	1.043	1.144	1.228	107
108		0.250	0.465	0.616	0.732	0.827	0.907	1.036	1.138	1.222	108
109		0.238	0.455	0.607	0.724	0.820	0.900	1.030	1.132	1.216	109
110		0.225	0.445	0.599	0.717	0.813	0.894	1.024	1.126	1.211	110
111		0.212	0.436	0.590	0.709	0.806	0.887	1.018	1.121	1.205	111
112		0.199	0.426	0.582	0.702	0.799	0.880	1.012	1.115	1.200	112
113		0.186	0.416	0.573	0.694	0.792	0.873	1.005	1.109	1.194	113
114		0.173	0.406	0.565	0.686	0.785	0.867	0.999	1.103	1.189	114
115		0.159	0.397	0.557	0.679	0.778	0.860	0.993	1.098	1.183	115
116		0.146	0.387	0.548	0.671	0.771	0.854	0.987	1.092	1.178	116
117		0.132	0.377	0.540	0.664	0.764	0.847	0.981	1.086	1.172	117
118		0.118	0.367	0.532	0.656	0.757	0.840	0.975	1.081	1.167	118
119		0.103	0.357	0.523	0.649	0.750	0.834	0.969	1.075	1.162	119
120		0.088	0.348	0.515	0.641	0.743	0.827	0.963	1.070	1.156	120
121		0.072	0.338	0.507	0.634	0.736	0.821	0.957	1.064	1.151	121
122		0.056	0.328	0.498	0.626	0.729	0.815	0.951	1.059	1.146	122
123		0.039	0.318	0.490	0.619	0.722	0.808	0.946	1.053	1.141	123
124		0.021	0.308	0.482	0.612	0.715	0.802	0.940	1.048	1.136	124
125			0.298	0.473	0.604	0.709	0.795	0.934	1.042	1.130	125
126			0.287	0.465	0.597	0.702	0.789	0.928	1.037	1.125	126
127			0.277	0.457	0.590	0.695	0.783	0.922	1.031	1.120	127
128			0.267	0.449	0.582	0.688	0.776	0.917	1.026	1.115	128
129			0.257	0.440	0.575	0.682	0.770	0.911	1.021	1.110	129
130			0.246	0.432	0.567	0.675	0.764	0.905	1.015	1.105	130
131			0.236	0.424	0.560	0.668	0.758	0.900	1.010	1.100	131
132			0.225	0.415	0.553	0.662	0.751	0.894	1.005	1.095	132
133			0.215	0.407	0.546	0.655	0.745	0.888	1.000	1.090	133
134			0.204	0.398	0.538	0.648	0.739	0.883	0.994	1.085	134
135			0.193	0.390	0.531	0.642	0.733	0.877	0.989	1.080	135
136			0.182	0.382	0.524	0.635	0.727	0.872	0.984	1.075	136
137			0.171	0.373	0.516	0.628	0.720	0.866	0.979	1.071	137
138			0.160	0.365	0.509	0.622	0.714	0.861	0.974	1.066	138
139			0.148	0.356	0.502	0.615	0.708	0.855	0.969	1.061	139
140			0.137	0.348	0.495	0.609	0.702	0.850	0.964	1.056	140
141			0.125	0.339	0.487	0.602	0.696	0.844	0.959	1.051	141
142			0.113	0.331	0.480	0.596	0.690	0.839	0.954	1.047	142
143			0.101	0.322	0.473	0.589	0.684	0.833	0.949	1.042	143
144			0.088	0.314	0.465	0.582	0.678	0.828	0.943	1.037	144
145			0.075	0.305	0.458	0.576	0.672	0.823	0.939	1.032	145
146			0.062	0.296	0.451	0.569	0.666	0.817	0.934	1.028	146
147			0.048	0.288	0.444	0.563	0.660	0.812	0.929	1.023	147
148			0.033	0.279	0.436	0.556	0.654	0.806	0.924	1.018	148
149			0.018	0.270	0.429	0.550	0.648	0.801	0.919	1.014	149

Table 2, continued

	100	125	150	175	200	225	250	300	350	400	
150				0.261	0.422	0.543	0.642	0.796	0.914	1.009	150
151				0.253	0.414	0.537	0.636	0.791	0.909	1.005	151
152				0.244	0.407	0.530	0.630	0.785	0.904	1.000	152
153				0.235	0.400	0.524	0.624	0.780	0.899	0.995	153
154				0.226	0.392	0.517	0.618	0.775	0.894	0.991	154
155				0.217	0.385	0.511	0.612	0.769	0.890	0.986	155
156				0.207	0.378	0.504	0.606	0.764	0.885	0.982	156
157				0.198	0.370	0.498	0.600	0.759	0.880	0.977	157
158				0.189	0.363	0.492	0.594	0.754	0.875	0.973	158
159				0.179	0.356	0.485	0.589	0.749	0.870	0.968	159
160				0.170	0.348	0.479	0.583	0.743	0.866	0.964	160
161				0.160	0.341	0.472	0.577	0.738	0.861	0.959	161
162				0.150	0.333	0.466	0.571	0.733	0.856	0.955	162
163				0.140	0.326	0.459	0.565	0.728	0.852	0.951	163
164				0.130	0.318	0.453	0.559	0.723	0.847	0.946	164
165				0.120	0.311	0.446	0.553	0.718	0.842	0.942	165
166				0.110	0.303	0.440	0.547	0.713	0.838	0.938	166
167				0.099	0.296	0.433	0.542	0.708	0.833	0.933	167
168				0.088	0.288	0.427	0.536	0.702	0.828	0.929	168
169				0.077	0.280	0.420	0.530	0.697	0.824	0.925	169
170				0.066	0.273	0.414	0.524	0.692	0.819	0.920	170
171				0.054	0.265	0.407	0.518	0.687	0.814	0.916	171
172				0.042	0.257	0.401	0.512	0.682	0.810	0.912	172
173				0.029	0.249	0.394	0.507	0.677	0.805	0.907	173
174				0.016	0.242	0.388	0.501	0.672	0.801	0.903	174
175					0.234	0.381	0.495	0.667	0.796	0.899	175
176					0.226	0.375	0.489	0.662	0.792	0.895	176
177					0.218	0.368	0.483	0.657	0.787	0.890	177
178					0.210	0.362	0.478	0.652	0.782	0.886	178
179					0.202	0.355	0.472	0.647	0.778	0.882	179
180					0.194	0.348	0.466	0.642	0.773	0.878	180
181					0.185	0.342	0.460	0.637	0.769	0.874	181
182					0.177	0.335	0.454	0.632	0.765	0.869	182
183					0.169	0.328	0.448	0.627	0.760	0.865	183
184					0.160	0.322	0.443	0.622	0.756	0.861	184
185					0.152	0.315	0.437	0.617	0.751	0.857	185
186					0.143	0.308	0.431	0.612	0.747	0.853	186
187					0.134	0.302	0.425	0.608	0.742	0.849	187
188					0.125	0.295	0.419	0.603	0.738	0.845	188
189					0.116	0.288	0.413	0.598	0.733	0.841	189
190					0.107	0.281	0.408	0.593	0.729	0.837	190
191					0.098	0.275	0.402	0.588	0.725	0.833	191
192					0.089	0.268	0.396	0.583	0.720	0.828	192
193					0.079	0.261	0.390	0.578	0.716	0.824	193
194					0.069	0.254	0.384	0.573	0.711	0.820	194
195					0.059	0.247	0.378	0.568	0.707	0.816	195
196					0.048	0.240	0.372	0.563	0.703	0.812	196
197					0.038	0.233	0.366	0.559	0.698	0.808	197
198					0.026	0.226	0.360	0.554	0.694	0.804	198
199					0.014	0.219	0.354	0.549	0.690	0.800	199

Table 2, continued

	225	250	300	350	400	
200	0.212	0.349	0.544	0.685	0.796	200
201	0.205	0.343	0.539	0.681	0.792	201
202	0.197	0.337	0.534	0.677	0.788	202
203	0.190	0.331	0.529	0.672	0.784	203
204	0.183	0.325	0.524	0.668	0.780	204
205	0.175	0.319	0.520	0.664	0.777	205
206	0.168	0.313	0.515	0.660	0.773	206
207	0.160	0.307	0.510	0.655	0.769	207
208	0.153	0.301	0.505	0.651	0.765	208
209	0.145	0.294	0.500	0.647	0.761	209
210	0.137	0.288	0.495	0.642	0.757	210
211	0.130	0.282	0.490	0.638	0.753	211
212	0.122	0.276	0.486	0.634	0.749	212
213	0.114	0.270	0.481	0.630	0.745	213
214	0.105	0.264	0.476	0.625	0.741	214
215	0.097	0.258	0.471	0.621	0.737	215
216	0.089	0.251	0.466	0.617	0.734	216
217	0.080	0.245	0.461	0.613	0.730	217
218	0.071	0.239	0.456	0.608	0.726	218
219	0.062	0.232	0.452	0.604	0.722	219
220	0.053	0.226	0.447	0.600	0.718	220
221	0.044	0.220	0.442	0.596	0.714	221
222	0.034	0.213	0.437	0.592	0.711	222
223	0.024	0.207	0.432	0.587	0.707	223
224	0.012	0.200	0.427	0.583	0.703	224
225		0.194	0.422	0.579	0.699	225
226		0.187	0.418	0.575	0.695	226
227		0.181	0.413	0.571	0.692	227
228		0.174	0.408	0.566	0.688	228
229		0.167	0.403	0.562	0.684	229
230		0.161	0.398	0.558	0.680	230
231		0.154	0.393	0.554	0.676	231
232		0.147	0.388	0.550	0.673	232
233		0.140	0.383	0.545	0.669	233
234		0.133	0.378	0.541	0.665	234
235		0.126	0.373	0.537	0.661	235
236		0.119	0.369	0.533	0.658	236
237		0.111	0.364	0.529	0.654	237
238		0.104	0.359	0.525	0.650	238
239		0.096	0.354	0.520	0.646	239
240		0.089	0.349	0.516	0.643	240
241		0.081	0.344	0.512	0.639	241
242		0.073	0.339	0.508	0.635	242
243		0.065	0.334	0.504	0.631	243
244		0.057	0.329	0.500	0.628	244
245		0.049	0.324	0.495	0.624	245
246		0.040	0.319	0.491	0.620	246
247		0.031	0.314	0.487	0.617	247
248		0.021	0.309	0.483	0.613	248
249		0.011	0.304	0.479	0.609	249

	300	350	400	
250	0.299	0.475	0.605	250
251	0.294	0.471	0.602	251
252	0.289	0.466	0.598	252
253	0.283	0.462	0.594	253
254	0.278	0.458	0.591	254
255	0.273	0.454	0.587	255
256	0.268	0.450	0.583	256
257	0.263	0.446	0.580	257
258	0.258	0.441	0.576	258
259	0.253	0.437	0.572	259
260	0.247	0.433	0.569	260
261	0.242	0.429	0.565	261
262	0.237	0.425	0.561	262
263	0.232	0.420	0.558	263
264	0.226	0.416	0.554	264
265	0.221	0.412	0.550	265
266	0.216	0.408	0.547	266
267	0.210	0.404	0.543	267
268	0.205	0.400	0.539	268
269	0.199	0.395	0.536	269
270	0.194	0.391	0.532	270
271	0.189	0.387	0.528	271
272	0.183	0.383	0.525	272
273	0.178	0.379	0.521	273
274	0.172	0.374	0.517	274
275	0.166	0.370	0.514	275
276	0.161	0.366	0.510	276
277	0.155	0.362	0.507	277
278	0.149	0.357	0.503	278
279	0.144	0.353	0.499	279
280	0.138	0.349	0.496	280
281	0.132	0.345	0.492	281
282	0.126	0.340	0.488	282
283	0.120	0.336	0.485	283
284	0.114	0.332	0.481	284
285	0.108	0.328	0.477	285
286	0.102	0.323	0.474	286
287	0.095	0.319	0.470	287
288	0.089	0.315	0.466	288
289	0.083	0.310	0.463	289
290	0.076	0.306	0.459	290
291	0.069	0.302	0.456	291
292	0.063	0.297	0.452	292
293	0.056	0.293	0.448	293
294	0.049	0.289	0.445	294
295	0.042	0.284	0.441	295
296	0.034	0.280	0.437	296
297	0.026	0.276	0.434	297
298	0.018	0.271	0.430	298
299	0.010	0.267	0.426	299

Table 2, continued

	350	400	
300	0.262	0.423	300
301	0.258	0.419	301
302	0.253	0.415	302
303	0.249	0.412	303
304	0.245	0.408	304
305	0.240	0.404	305
306	0.236	0.401	306
307	0.231	0.397	307
308	0.226	0.393	308
309	0.222	0.390	309
310	0.217	0.386	310
311	0.213	0.382	311
312	0.208	0.379	312
313	0.204	0.375	313
314	0.199	0.371	314
315	0.194	0.368	315
316	0.189	0.364	316
317	0.185	0.360	317
318	0.180	0.356	318
319	0.175	0.353	319
320	0.170	0.349	320
321	0.166	0.345	321
322	0.161	0.342	322
323	0.156	0.338	323
324	0.151	0.334	324
325	0.146	0.330	325
326	0.141	0.327	326
327	0.136	0.323	327
328	0.131	0.319	328
329	0.126	0.315	329
330	0.121	0.312	330
331	0.116	0.308	331
332	0.111	0.304	332
333	0.105	0.300	333
334	0.100	0.296	334
335	0.095	0.293	335
336	0.089	0.289	336
337	0.084	0.285	337
338	0.078	0.281	338
339	0.072	0.277	339
340	0.067	0.274	340
341	0.061	0.270	341
342	0.055	0.266	342
343	0.049	0.262	343
344	0.043	0.258	344
345	0.036	0.254	345
346	0.030	0.250	346
347	0.023	0.246	347
348	0.016	0.242	348
349	0.008	0.238	349

	400	
350	0.235	350
351	0.231	351
352	0.227	352
353	0.223	353
354	0.219	354
355	0.215	355
356	0.211	356
357	0.207	357
358	0.202	358
359	0.198	359
360	0.194	360
361	0.190	361
362	0.186	362
363	0.182	363
364	0.178	364
365	0.174	365
366	0.169	366
367	0.165	367
368	0.161	368
369	0.157	369
370	0.152	370
371	0.148	371
372	0.144	372
373	0.139	373
374	0.135	374
375	0.131	375
376	0.126	376
377	0.122	377
378	0.117	378
379	0.113	379
380	0.108	380
381	0.103	381
382	0.099	382
383	0.094	383
384	0.089	384
385	0.084	385
386	0.080	386
387	0.075	387
388	0.070	388
389	0.065	389
390	0.059	390
391	0.054	391
392	0.049	392
393	0.043	393
394	0.038	394
395	0.032	395
396	0.026	396
397	0.020	397
398	0.014	398
399	0.007	399
400	-----	400

Table 3. Standardized selection differential when population size is infinite.

Proportion Selected	.000	.001	.002	.003	.004	.005	.006	.007	.008	.009
.00	-----	3.367	3.170	3.050	2.962	2.892	2.834	2.784	2.740	2.701
.01	2.665	2.633	2.603	2.575	2.549	2.525	2.502	2.480	2.459	2.440
.02	2.421	2.403	2.386	2.369	2.353	2.338	2.323	2.309	2.295	2.281
.03	2.268	2.255	2.243	2.231	2.219	2.208	2.197	2.186	2.175	2.165
.04	2.154	2.144	2.135	2.125	2.116	2.106	2.097	2.088	2.080	2.071
.05	2.063	2.054	2.046	2.038	2.030	2.023	2.015	2.007	2.000	1.993
.06	1.985	1.978	1.971	1.964	1.957	1.951	1.944	1.937	1.931	1.924
.07	1.918	1.912	1.906	1.899	1.893	1.887	1.881	1.876	1.870	1.864
.08	1.858	1.853	1.847	1.842	1.836	1.831	1.825	1.820	1.815	1.810
.09	1.804	1.799	1.794	1.789	1.784	1.799	1.774	1.769	1.765	1.760
.10	1.755	1.750	1.746	1.741	1.736	1.732	1.727	1.723	1.718	1.714
.11	1.709	1.705	1.701	1.696	1.692	1.688	1.684	1.679	1.675	1.671
.12	1.667	1.663	1.659	1.655	1.651	1.647	1.643	1.639	1.635	1.631
.13	1.627	1.623	1.620	1.616	1.612	1.608	1.605	1.601	1.597	1.593
.14	1.590	1.586	1.583	1.579	1.575	1.572	1.568	1.565	1.561	1.558
.15	1.554	1.551	1.548	1.544	1.541	1.537	1.534	1.531	1.527	1.524
.16	1.521	1.517	1.514	1.511	1.508	1.504	1.501	1.498	1.495	1.492
.17	1.489	1.485	1.482	1.479	1.476	1.473	1.470	1.467	1.464	1.461
.18	1.458	1.455	1.452	1.449	1.446	1.443	1.440	1.437	1.434	1.431
.19	1.428	1.425	1.422	1.420	1.417	1.414	1.411	1.408	1.405	1.403
.20	1.400	1.397	1.394	1.391	1.389	1.386	1.383	1.381	1.378	1.375
.21	1.372	1.370	1.367	1.364	1.362	1.359	1.356	1.354	1.351	1.348
.22	1.346	1.343	1.341	1.338	1.336	1.333	1.330	1.328	1.325	1.323
.23	1.320	1.318	1.315	1.313	1.310	1.308	1.305	1.303	1.300	1.298
.24	1.295	1.293	1.290	1.288	1.286	1.283	1.281	1.278	1.276	1.273
.25	1.271	1.269	1.266	1.264	1.262	1.259	1.257	1.255	1.252	1.250
.26	1.248	1.245	1.243	1.241	1.238	1.236	1.234	1.231	1.229	1.227
.27	1.225	1.222	1.220	1.218	1.216	1.213	1.211	1.209	1.207	1.204
.28	1.202	1.200	1.198	1.196	1.193	1.191	1.189	1.187	1.185	1.183
.29	1.180	1.178	1.176	1.174	1.172	1.170	1.167	1.165	1.163	1.161
.30	1.159	1.157	1.155	1.153	1.151	1.148	1.146	1.144	1.142	1.140
.31	1.138	1.136	1.134	1.132	1.130	1.128	1.126	1.124	1.122	1.120
.32	1.118	1.116	1.113	1.111	1.109	1.107	1.105	1.103	1.101	1.099
.33	1.097	1.095	1.093	1.091	1.089	1.088	1.086	1.084	1.082	1.080
.34	1.078	1.076	1.074	1.072	1.070	1.068	1.066	1.064	1.062	1.060
.35	1.058	1.056	1.054	1.053	1.051	1.049	1.047	1.045	1.043	1.041
.36	1.039	1.037	1.035	1.034	1.032	1.030	1.028	1.026	1.024	1.022
.37	1.020	1.019	1.017	1.015	1.013	1.011	1.009	1.007	1.006	1.004
.38	1.002	1.000	0.998	0.997	0.995	0.993	0.991	0.989	0.987	0.986
.39	0.984	0.982	0.980	0.978	0.977	0.975	0.973	0.971	0.969	0.968
.40	0.966	0.964	0.962	0.961	0.959	0.957	0.955	0.953	0.952	0.950
.41	0.948	0.946	0.945	0.943	0.941	0.939	0.938	0.936	0.934	0.932
.42	0.931	0.929	0.927	0.926	0.924	0.922	0.920	0.919	0.917	0.915
.43	0.913	0.912	0.910	0.908	0.907	0.905	0.903	0.902	0.900	0.898
.44	0.896	0.895	0.893	0.891	0.890	0.888	0.886	0.885	0.883	0.881
.45	0.880	0.878	0.876	0.875	0.873	0.871	0.870	0.868	0.866	0.865
.46	0.863	0.861	0.860	0.858	0.856	0.855	0.853	0.851	0.850	0.848
.47	0.846	0.845	0.843	0.841	0.840	0.838	0.837	0.835	0.833	0.832
.48	0.830	0.828	0.827	0.825	0.824	0.822	0.820	0.819	0.817	0.816
.49	0.814	0.812	0.811	0.809	0.807	0.806	0.804	0.803	0.801	0.799

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Table 3, continued

Proportion Selected	.000	.001	.002	.003	.004	.005	.006	.007	.008	.009
.50	0.798	0.746	0.795	0.793	0.792	0.790	0.788	0.787	0.785	0.784
.51	0.782	0.780	0.779	0.777	0.776	0.774	0.773	0.771	0.769	0.768
.52	0.766	0.765	0.763	0.762	0.760	0.758	0.757	0.755	0.754	0.752
.53	0.751	0.749	0.747	0.746	0.744	0.743	0.741	0.740	0.738	0.737
.54	0.735	0.734	0.732	0.730	0.729	0.727	0.726	0.724	0.723	0.721
.55	0.720	0.718	0.717	0.715	0.714	0.712	0.710	0.709	0.707	0.706
.56	0.704	0.703	0.701	0.700	0.698	0.697	0.695	0.694	0.692	0.691
.57	0.689	0.688	0.686	0.685	0.683	0.682	0.680	0.678	0.677	0.675
.58	0.674	0.672	0.671	0.669	0.668	0.666	0.665	0.663	0.662	0.660
.59	0.659	0.657	0.656	0.654	0.653	0.651	0.650	0.648	0.647	0.645
.60	0.644	0.642	0.641	0.639	0.638	0.636	0.635	0.633	0.632	0.630
.61	0.629	0.627	0.626	0.625	0.623	0.622	0.620	0.619	0.617	0.616
.62	0.614	0.613	0.611	0.610	0.608	0.607	0.605	0.604	0.602	0.601
.63	0.599	0.598	0.596	0.595	0.593	0.592	0.590	0.589	0.588	0.586
.64	0.585	0.583	0.582	0.580	0.579	0.577	0.576	0.574	0.573	0.571
.65	0.570	0.568	0.567	0.565	0.564	0.563	0.561	0.560	0.558	0.557
.66	0.555	0.554	0.552	0.551	0.549	0.548	0.546	0.545	0.543	0.542
.67	0.541	0.539	0.538	0.536	0.535	0.533	0.532	0.530	0.529	0.527
.68	0.526	0.524	0.523	0.522	0.520	0.519	0.517	0.516	0.514	0.513
.69	0.511	0.510	0.508	0.507	0.505	0.504	0.503	0.501	0.500	0.498
.70	0.497	0.495	0.494	0.492	0.491	0.489	0.488	0.486	0.485	0.484
.71	0.482	0.481	0.479	0.478	0.476	0.475	0.473	0.472	0.470	0.469
.72	0.468	0.466	0.465	0.463	0.462	0.460	0.459	0.457	0.456	0.454
.73	0.453	0.451	0.450	0.449	0.447	0.446	0.444	0.443	0.441	0.440
.74	0.438	0.437	0.435	0.434	0.432	0.431	0.430	0.428	0.427	0.425
.75	0.424	0.422	0.421	0.419	0.418	0.416	0.415	0.413	0.412	0.411
.76	0.409	0.408	0.406	0.405	0.403	0.402	0.400	0.399	0.397	0.396
.77	0.394	0.393	0.391	0.390	0.388	0.387	0.386	0.384	0.383	0.381
.78	0.380	0.378	0.377	0.375	0.374	0.372	0.371	0.369	0.368	0.366
.79	0.365	0.363	0.362	0.360	0.359	0.357	0.356	0.354	0.353	0.351
.80	0.350	0.348	0.347	0.345	0.344	0.342	0.341	0.340	0.338	0.337
.81	0.335	0.334	0.332	0.331	0.329	0.328	0.326	0.325	0.323	0.322
.82	0.320	0.318	0.317	0.315	0.314	0.312	0.311	0.309	0.308	0.306
.83	0.305	0.303	0.302	0.300	0.299	0.297	0.296	0.294	0.293	0.291
.84	0.290	0.288	0.287	0.285	0.284	0.282	0.280	0.279	0.277	0.276
.85	0.274	0.273	0.271	0.270	0.268	0.267	0.265	0.263	0.262	0.260
.86	0.259	0.257	0.256	0.254	0.253	0.251	0.249	0.248	0.246	0.245
.87	0.243	0.242	0.240	0.238	0.237	0.235	0.234	0.232	0.231	0.229
.88	0.227	0.226	0.224	0.223	0.221	0.219	0.218	0.216	0.215	0.213
.89	0.211	0.210	0.208	0.206	0.205	0.203	0.202	0.200	0.198	0.197
.90	0.195	0.193	0.192	0.190	0.188	0.187	0.185	0.183	0.182	0.180
.91	0.178	0.177	0.175	0.173	0.172	0.170	0.168	0.167	0.165	0.163
.92	0.162	0.160	0.158	0.156	0.155	0.153	0.151	0.150	0.148	0.146
.93	0.144	0.143	0.141	0.139	0.137	0.136	0.134	0.132	0.130	0.129
.94	0.127	0.125	0.123	0.121	0.120	0.118	0.116	0.114	0.112	0.110
.95	0.109	0.107	0.105	0.103	0.101	0.099	0.097	0.095	0.094	0.092
.96	0.090	0.088	0.086	0.084	0.082	0.080	0.078	0.076	0.074	0.072
.97	0.070	0.068	0.066	0.064	0.062	0.060	0.058	0.056	0.054	0.052
.98	0.049	0.047	0.045	0.043	0.041	0.038	0.036	0.034	0.032	0.029
.99	0.027	0.025	0.022	0.020	0.017	0.015	0.012	0.009	0.006	0.003

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