MANUAL OF

QUANTITATIVE

GENETICS

WALTER A. BECKER
Fourth Edition

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by

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PREFACE

This is the fourth edition of this Manual. It originally was written as a laboratory manual for a quantitative genetics class at Washington State University in 1961. The first edition was published in 1964 and several other editions were printed as new material became available.

The format was designed for use with a text such as Falconer's "Introduction to Quantitative Genetics". With content expansion, investigators have found it useful as a handy reference book.

When the third edition went out of print, a decision was made not to publish more editions because of the impression that the advent of computers made the Manual superfluous. Apparently the Manual meets a need for explanation of the procedures used in quantitative genetics because orders kept arriving at the Washington State University Press and the Student Book Corporation.

This fourth edition has been prepared with several changes in procedures, and the addition of new references and books. It will be sold by direct mail order through Academic Enterprises.

The first printing of the fourth edition sold out in four months and this first reprinting incorporates new references and material. The paper and covers consist of heavier stock than the first printing and the typography has been improved.

In the Manual, the statistical model within each procedure is given first, and then the genetic meaning of the various components of the model. The statistical formulas for computing the procedures are presented, usually with a worked example.

Throughout the manual the dot notation has been utilized in the formulas. References are made to more advanced or other procedures which might be of use to the student or researcher.

Many colleagues wrote and pointed out misprints and made useful suggestions for improving the manual. Especially helpful were Thomas P. Bogyo, James R. Chambers, Everett R. Dempster, Michael Grossman, Holly Hartman, Larry Mirosh and Jingxiang Ou.

Others also mentioned possible corrections and improvements for which I am grateful. Anyone finding an error is encouraged to write to the author so that future reprintings may be corrected.

Certain pages (see pg. 18) have been deliberately left blank so that major sections could begin on a right hand page.

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Pullman, Washington

SYMBOLS

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

I. Statistical symbols

Symbol	Meaning
X_i or Y_i	the ith observation
X_1, X_2	the first observation, second observation
Z_i	the ith 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 kth observation in the ith and j^{th} classification. Example: the kth progeny of the ith sire mated to the jth dam.
$\frac{1}{n} \sum_i Y_i = \frac{Y.}{n} = \bar{y}.$	the sample mean of n observations
var	variance
cov	covariance
b	regression coefficient
coeff.	coefficient
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
S.E.	standard error

$<$	is less than
$>$	is greater than
$\geq$	is greater than or equal to
$\leq$	is less than or equal to
$\cong$	approximates
$\neq$	not equal
σ^2	variance
σ	standard deviation
α, β, δ, e, γ	used in statistical models for source of variation; they are defined in the text when used

Greek letters refer to parameters, Greek letters with a circumflex or "hat" refer to estimates of those parameters, e.g., $\hat{\sigma}^2$ = estimate of the variance.

The word "between" will be used throughout the manual to designate sources of variation (i.e., Between Sires, Between Dams within Sires) even when more than two units are involved.

II. Genetic symbols

These symbols are similiar to those used in Falconer (1981).

Symbol	Meaning
V_G	genotypic variance where $V_G = V_A + V_D + V_I$
V_A	additive genetic variance
V_{AM}	assortative mating 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_{EC}	variance of effects common to families other than maternal, i.e., cage, pen effects or plot effects
V_M	maternal effects variance
V_{LM}	sex linkage variance of males
V_{LF}	sex linkage variance of females
V_{GE}	genotype x environment interaction
V_P	phenotypic variance
$cov_{A(X_1 X_2)}$	additive genetic covariance between traits X_1 and X_2
$cov_{D(X_1 X_2)}$	dominance covariance between traits X_1 and X_2
$cov_{E(X_1 X_2)}$	environmental covariance between traits X_1 and X_2
$cov_{P(X_1 X_2)}$	phenotypic covariance between traits X_1 and X_2
$cov_{relatives}$	covariance between relatives
cov_{HS}	covariance between half sibs
cov_{FS}	covariance between full sibs
cov_{OP}	covariance between offspring and parent
r_G	genetic correlation
r_P	phenotypic correlation
r_E	environmental correlation
α	coefficient for additive genetic effects
δ	coefficient for dominance effects
Δ	change; designates selection gain
F	inbreeding coefficient

h^2	additive heritability
$h_G^{\ 2}$	genotypic heritability
i	selection intensity; selection differential in standard deviations
DZ	dizygous twins
MZ	monozygous twins
R	repeatability
S	selection differential

In general, the statistical models use the statistical symbols while the genetic interpretation of those models will use the genetic symbols. Usually, a symbol will have the same meaning throughout the manual. There are some symbols which are given two or more meanings. An example is α which designates source of variation, usually sire, in the statistical models while α in the genetic models means coefficient for additive genetic effects. When this class of symbols is used, definitions are provided in the manual so its meaning is clear.

GENERAL ASSUMPTIONS

Reference Population

All procedures provide estimates which refer to a base reference population. This reference population should be defined in every experiment and all inferences made about the estimates should depend upon the composition of the reference population.

This reference population may consist of a random-bred flock of Beltsville White turkeys, all the Holstein cows and bulls involved in a DHIA program, a specific herd of Hereford cattle, all Douglas Fir trees on the western slope of the Cascade Mountains in the states of Washington and Oregon, all rainbow trout in a specific drainage, or a large open-pollinated variety of Zea mays.

When inbred lines are crossed and the covariance of relatives determined, the estimates of genetic variances and covariances are applicable to the reference population which would be the original population from which the inbred lines were derived.

Linkage

It is assumed that there is no autosomal linkage of genes affecting the observed trait. If linkage does exist then the epistatic components of the covariance of relatives may be affected (Schnell, 1963).

Diploid Mendelian Inheritance

There is no interference with segregation and independent assortment of the chromosomes. Diploidy of cross fertilized plants and animals is assumed throughout. For polyploidy see Kempthorne (1955).

No Selection During Formation of Inbred Lines

When inbred lines are crossed and estimates are made of genetic parameters pertaining to the reference population from which the inbred lines were derived, an assumption is made that the inbred lines were not selected. When this assumption is violated then the estimates of genetic variances no longer pertain to the reference population because the gene frequencies have changed. This type of situation frequently occurs in plant breeding.

Inbreeding of the Reference Population

The assumption is made that the inbreeding coefficient of the reference population is zero. With more than two loci and no epistasis, a large number of parameters are involved when a reference population is inbred. With epistasis, the analysis is very complex (Harris, 1964).

General References

These and other assumptions have been discussed by Cockerham (1963) and Kuehl et al. (1968). The inadequacy of quantitative genetics as it relates to the prediction of selection gains and correlated responses has been detailed by Robertson (1966) and by Lee and Parsons (1968). A general review has been made by Barker (1967).

For a discussion of laboratory and domestic animal selection experiments see Robertson (ed) (1980). Harris et al. (1984) provide a systematic approach to the design of animal breeding programs. A short review of forest tree improvement and a list of many useful references is given by van Buijtenen et al. (1981).

COVARIANCE OF RELATIVES

I. Relationships (Malecot, 1948)

    A. Coefficients

        1. Additive genetic effects

$$\alpha = \frac{\phi + \phi'}{2}$$

        where α = coefficient for additive genetic effects.

        ϕ = probability that paternal allele in one relative is identical to an allele in other relative.

        ϕ' = probability that maternal allele in one relative is identical to an allele in other relative.

        2. Dominance effects

$$\delta = \phi \, \phi'$$

        where δ = coefficient for dominance effects.

    B. Coefficients for relatives

        1. Half sibs (common father or mother)

$$\alpha = \frac{1/2 + 0}{2} = 1/4$$

$$\delta = (1/2)(0) = 0$$

        2. Full sibs

$$\alpha = \frac{1/2 + 1/2}{2} = 1/2$$

$$\delta = (1/2)(1/2) = 1/4$$

        3. Parent-offspring

$$\alpha = \frac{1 + 0}{2} = 1/2$$

$$\delta = (1)(0) = 0$$

        4. Monozygotic twins and clones

$$\alpha = \frac{1 + 1}{2} = 1$$

$$\delta = (1)(1) = 1$$

The table below summarizes these relationships.

Relationship	α	δ
Monozygotic twins or clones	1	1
Dizygous twins or full sibs	1/2	1/4
Half sibs	1/4	0
First cousins	1/8	0
Double first cousins	1/4	1/16
Parent-offpsring	1/2	0
Grandparent-grandchild	1/4	0
Aunt-niece	1/4	0
Uncle-nephew	1/4	0

The genetic information about an individual furnished by the knowl-edge of the genotype of a relative has been considered by Jacquard (1972) who used a set of nine condensed identity coefficients. Cal-culations using these type of coefficients have been given by Nadot and Vaysseix (1973). •

II. Estimation of genetic variances

A. General formula

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

where $cov_{relatives}$ is the covariance between relatives and can be interpreted in terms of genetic variances by the above equation.

B. Table of covariances and genetic variances

Covariance	V_A	V_D	V_{AA}	V_{AD}	V_{DD}	V_{AAA}
cov (clones)	1	1	1	1	1	1
cov (full sibs)	1/2	1/4	1/4	1/8	1/16	1/8
cov (half sibs)	1/4	0	1/16	0	0	1/64
cov (first cousins)	1/8	0	1/64	0	0	1/512
cov (double first cousins)	1/4	1/16	1/16	1/64	1/256	1/64
cov (parent-offspring)	1/2	0	1/4	0	0	1/8
cov (grandparent-grandchild)	1/4	0	1/16	0	0	1/64
cov (aunt-niece)	1/4	0	1/16	0	0	1/64
cov (uncle-nephew)	1/4	0	1/16	0	0	1/64
cov (general)	α	δ	α^2	$\alpha\delta$	δ^2	α^3

The covariance of relatives in various experimental designs is given by Cockerham (1963). Maternal influences on the covariance of relatives have been considered by Willham (1963).

C. Sex linkage

When one sex is heterogametic, the covariance between relatives of unlike sex (sire-daughter, dam-son) has an element in addition to the table given above. The homogametic sex is diploid while the heterogametic sex is monoploid (James, 1973).

	Sex of Offspring			
	Male Heterogametic		Female Heterogametic	
Covariance	Male	Female	Male	Female
Sire-offspring	0	cov_{MF}	$1/2\ V_{LM}$	cov_{MF}
Dam-offspring	cov_{MF}	$1/2\ V_{LF}$	cov_{MF}	0
Midparent-offspring	$1/2\ cov_{MF}$	$1/4\ V_{LF} + 1/2\ cov_{MF}$	$1/4\ V_{LM} + 1/2\ cov_{MF}$	$1/2\ cov_{MF}$
Variance components				
Full sibs	$1/2\ V_{LM}$	$3/4\ V_{LF}$	$3/4\ V_{LM}$	$1/2\ V_{LF}$
Sires	0	$1/2\ V_{LF}$	$1/4\ V_{LM}$	$1/2\ V_{LF}$
Dams	$1/2\ V_{LM}$	$1/4\ V_{LF}$	$1/2\ V_{LM}$	0

Source: James, J. W. (1973).

All variances and covariances refer to the additive genetic component. Because the variances will be different for the diploid and monoploid populations, the variances are given in terms of the female population, V_{LF}, and male population, V_{LM}.

Variance components for dam and sires do not change when nested.

III. Covariance of hybrid relatives

When two inbred lines derived from the same reference population are crossed, the covariance of the hybrid relatives must take into account the amount of inbreeding.

A. Single cross

1. Single individuals from each line used for crossing

$$\phi = 1/2 + F/2 = \frac{1 + F}{2}$$

$$\phi' = 1/2 + F/2 = \frac{1 + F}{2}$$

$$\alpha = \frac{\phi + \phi'}{2} = \frac{\frac{1+F}{2} + \frac{1+F}{2}}{2} = \frac{1+F}{2}$$

$$\delta = \phi\,\phi' = \left(\frac{1+F}{2}\right)^2$$

2. Several individuals from each line used for crossing. For example, bulked pollen.

$$\phi = F$$

$$\phi' = F$$

$$\alpha = \frac{F+F}{2} = F$$

$$\delta = (F)(F) = F^2$$

B. Three way crosses

Several individuals from each line used for crossing.

$$\phi \ (\text{single line}) = F$$

$$\phi' \ (\text{single cross}) = F/2$$

$$\alpha = \frac{F + F/2}{2} = 3F/4$$

$$\delta = F \times F/2 = F^2/2$$

C. Double crosses

Two single crosses with several individuals per line are crossed together.

$$\phi = F/2$$

$$\phi' = F/2$$

$$\alpha = \frac{F/2 + F/2}{2} = F/2$$

$$\delta = (F/2)(F/2) = F^2/4$$