

SEX-LINKED AND MATERNAL EFFECTS IN THE DIALLEL CROSS*

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Summary

The diallel cross has been used frequently in plant experiments to partition the genetic variation into general and specific combining abilities of inbred lines. The statistical models developed for analysis of diallel crosses in plants have been used in a number of studies of diallel crosses in mammals and poultry, without due consideration to the presence and effect of the sex chromosomes.

Two statistical models for the analysis of the modified diallel cross, one assuming maternal effects and one assuming no maternal effects, were compared for male and female progeny of both male homogametic species and female homogametic species. It was found that neither statistical model is adequate to separate the effects of sex-linked genes from both maternal and autosomal additive genetic effects when data on only one sex of progeny are analysed.

Utilization of estimates from both statistical models provides a crude estimate of sex-linked, maternal, and additive autosomal effects only in the case of female progeny of male homogametic species such as poultry.

I. INTRODUCTION

Sex-linked and maternal effects are the primary sources of reciprocal differences in animal breeding experiments. These reciprocal differences generally are considered to be of little importance in plant material (Griffing 1956). The presence of these reciprocal effects are important in deciding upon the use of either the sire or dam of a line in a cross. Cock and Morton (1963) suggested the use of the diallel cross in poultry as a method of partitioning these reciprocal differences into sex-linked and maternal sources of variation. Schaffer and Kojima (1963) employed a variant of the diallel cross to obtain estimates of sex-linked effects for wing length in *Drosophila pseudoobscura*.

The problems of estimating sex-linked and maternal effects are considered for the modified diallel experiment.

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II. THEORETICAL DEVELOPMENT

(a) *Analysis in Terms of Existing Models*

We consider a diallel cross wherein p inbred parent lines are crossed in all combinations, such that $p(p-1)$ single-cross progeny groups are obtained. The layout of such an experiment is given in Table 1. The value X_{ij} represents the mean of

TABLE 1
EXPERIMENTAL DESIGN OF A MODIFIED DIALLEL CROSS AMONG
 p INBRED LINES

		Inbred Line—Dams				Sire Totals
		1	2	...	p	
Inbred Line—Sires	1		X_{12}	...	X_{1p}	$X_{1.}$
	2	X_{21}			X_{2p}	$X_{2.}$

	p	X_{p1}	X_{p2}			$X_{p.}$
Dam totals		$X_{.1}$	$X_{.2}$		$X_{.p}$	$X_{..}$

a cross between sire line i and dam line j . Since the parental crosses are missing, let us denote by $\sum_{j \in Z_i}$ the operation of summation over the index set $(1, 2, \dots, p)$ exclusive of the index i , i.e. define

$$Z_i = (1, 2, \dots, i-1, i+1, \dots, p).$$

We now write the marginal sums as

$$X_{i.} = \sum_{j \in Z_i} X_{ij},$$

$$X_{.j} = \sum_{i \in Z_i} X_{ij},$$

and the grand sum as

$$X_{..} = \sum_{i=1}^p X_{i.} = \sum_{j=1}^p X_{.j}.$$

The experiment may be analysed in terms of the models presented by Henderson (1948) and Griffing (1956), which are henceforth referred to as model A and model B, respectively. Model A is given by

$$X_{ij} = \mu + g_i^* + g_j^* + m_j^* + r_{ij}^* + s_{ij}^* + e_{ij},$$

where X_{ij} = the mean progeny performance of a mating between a sire in line i and a dam in line j ; $i, j = 1, \dots, p$ (the number of progeny per mating is assumed constant),

- μ = the grand mean,
 $g_i^*(g_j^*)$ = the general combining ability effect of the i th(j th) line,
 m_j^* = the "maternal" effect of the j th line,
 s_{ij}^* = the specific combining ability effect of the (ij) th cross,
 r_{ij}^* = the residual effect of a difference between the (ij) th reciprocal crosses, and
 e_{ij} = the random error.

The linear restrictions on the parameters in model A are given by:

$$\sum_i g_i^* = \sum_j m_j^* = \sum_{j \in Z_i} s_{ij}^* = \sum_{j \in Z_i} r_{ij}^* = 0, \quad r_{ij}^* = -r_{ji}^*, \quad \text{and} \quad s_{ij}^* = s_{ji}^*.$$

If the lines are assumed fixed, then interest lies in the least-squares estimates of the parameters in the model (Henderson 1948), which are given by

$$\begin{aligned} \hat{\mu} &= \frac{X_{..}}{p(p-1)}, \\ \hat{g}_i^* &= \frac{1}{p(p-2)} \left[(p-1)X_{i.} + X_{.i} - X_{..} \right], \\ \hat{m}_j^* &= \frac{1}{p} (X_{.j} - X_{j.}), \\ \hat{r}_{ij}^* &= \frac{1}{2p} \left[p(X_{ij} - X_{ji}) + (X_{.i} - X_{.j} - X_{i.} + X_{j.}) \right], \\ \hat{s}_{ij}^* &= \frac{1}{2} (X_{ij} + X_{ji}) - \frac{1}{2(p-2)} (X_{i.} + X_{.i} + X_{j.} + X_{.j}) + \frac{X_{..}}{(p-1)(p-2)}. \end{aligned}$$

Note that the parental sums $X_{i.}$ and $X_{.i}$ in the expression for \hat{g}_i^* are weighted unequally in favour of the male parent in order to adjust the average effect of the i th line for marginal reciprocal differences, which Henderson (1948) attributed to maternal influences of the dam line.

Henderson's method utilizes the general least-squares procedure. Even though the estimates and their associated sums of squares are based on balanced data (i.e. equal numbers of progeny per cross), the various sets of estimates are statistically interdependent and the corresponding sums of squares are not mutually independent. In the case of fixed lines, hypothesis testing proceeds sequentially, the proper error term for a given hypothesis being dependent upon the decision reached in the previous test, within the limits of good pooling practices (Henderson 1948). In the case of random lines, the various sums of squares are set equal to their expectation and estimates of variance components are obtained in the usual way (Henderson 1948; King and Henderson 1954). Since no orthogonal analysis exists in either case, no tabular display of the Henderson technique will be given.

Model B is based on the diallel analysis proposed by Griffing (1956), which may be written

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

where X_{ij} , μ , s_{ij} , and e_{ij} are defined as in model A; moreover, μ and s_{ij} have the

TABLE 2
ANALYSIS OF VARIANCE OF A MODIFIED DIALLEL EXPERIMENT FOR MODEL B

Source of Variation	Degrees of Freedom	Sum of Squares (S.S.)	Mean Square (M.S.)	Expectations of Mean Squares	
				Fixed Model	Random Model
General combining ability (g.c.a.)	$p-1$	$S.S._{g.c.a.}$	$M.S._{g.c.a.}$	$\sigma^2 + 2(p-2)\{[1/(p-1)] \sum_i g_i^2\}$	$\sigma^2 + 2\sigma_g^2 + 2(p-2)\sigma_d^2$
Specific combining ability (s.c.a.)	$\frac{1}{2}p(p-3)$	$S.S._{s.c.a.}$	$M.S._{s.c.a.}$	$\sigma^2 + 2\{[2/p(p-3)] \sum_{i < j} s_{ij}^2\}$	$\sigma^2 + 2\sigma_s^2$
Reciprocal effects (r)	$\frac{1}{2}p(p-1)$	$S.S._r$	$M.S._r$	$\sigma^2 + 2\{[2/p(p-1)] \sum_{i < j} r_{ij}^2\}$	$\sigma^2 + 2\sigma_r^2$
Error (w)	$N - p^2 - p - 1$	$S.S._w$	$M.S._w$	σ^2	σ^2

where

$$S.S._{g.c.a.} = \frac{1}{2(p-2)} \sum_i (X_{i.} + X_{.i})^2 - \frac{2}{p(p-2)} X_{..}^2,$$

$$S.S._{s.c.a.} = \frac{1}{2} \sum_{i < j} \sum (X_{ij} + X_{ji})^2 - \frac{1}{2(p-2)} \sum_i (X_{i.} + X_{.i})^2 + \frac{1}{(p-1)(p-2)} X_{..}^2,$$

$$S.S._r = \frac{1}{2} \sum_{i < j} \sum (X_{ij} - X_{ji})^2.$$

same least-squares estimates as in model A. The analysis of variance, which is orthogonal, and the expected mean squares for model B are given in Table 2.

The difference between the definitions of g_i and r_{ij} on the one hand and g_i^* , m_j^* , and r_{ij}^* on the other may be seen by comparing least-squares estimates. The least-squares estimates in model B are (Griffing 1956):

$$\hat{g}_i = \frac{1}{2p(p-2)} \left[p(X_{i.} + X_{.i}) - 2X_{..} \right],$$

$$\hat{r}_{ij} = \frac{1}{2}(X_{ij} - X_{ji}).$$

The estimates of general combining ability effects for model B are symmetrical, since the model assumes no additive maternal effect *per se*.

The mathematical relationship between the least-squares estimates follows. Note that the least-squares estimate of the reciprocal effect in model A is given by

$$\hat{r}_{ij}^* = \frac{1}{2}(X_{ij} - X_{ji}) + \frac{1}{2p}(X_{.i} - X_{i.}) - \frac{1}{2p}(X_{.j} - X_{j.})$$

$$= \hat{r}_{ij} + \frac{1}{2}\hat{m}_i^* - \frac{1}{2}\hat{m}_j^*,$$

and the least-squares estimate of the general combining ability effect is

$$\hat{g}_i^* = \frac{1}{p(p-2)} \left[(p-1)X_{i.} + X_{.i} - X_{..} \right]$$

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

$$= \hat{g}_i - \frac{1}{2}\hat{m}_i^*.$$

Thus, model A may be rewritten as

$$X_{ij} = \mu + (g_i - \frac{1}{2}m_i^*) + (g_j - \frac{1}{2}m_j^*) + m_j^* + (r_{ij} + \frac{1}{2}m_i^* - \frac{1}{2}m_j^*) + s_{ij} + e_{ij}.$$

It is clear that m_j^* is in fact an average or general reciprocal effect, due solely to differences in the marginal means of sires and dams of a line. Although r_{ij} is a reciprocal effect, it contains a portion of the marginal effects. On the other hand, r_{ij}^* may be termed a residual reciprocal effect.

(b) Proposed Models

The distinction between the parameters of models A and B will now be clarified from a genetic standpoint. Griffing (1956) indicates that the more common type of diallel design with plant material does not involve reciprocal F_1 crosses, since maternal and sex-linked effects are usually absent. When dealing with mammals and birds, these reciprocal effects may be important in deciding upon the use of either sires or dams of a line in developing commercially superior crossbred progeny. Where interpretations concerning sex-linked and maternal effects in diallel analyses have been made (e.g. Henderson 1948; Goto and Nordskog 1959), no apparent consideration has been given as to whether:

- (1) The male or female of the species was the homogametic sex.
- (2) The trait was measured on male or female progeny or both.

On the other hand, Schaffer and Kojima (1963) considered the sex of progeny when using the diallel cross, in conjunction with other methods, for the detection of sex-linked effects on a quantitative trait of *Drosophila pseudoobscura*. Similarly, Cock and Morton (1963) reviewed the contradictory interpretations in the literature with respect to sex-linked and maternal effects in poultry, and suggested a diallel design for the purpose of detecting these effects. This problem was also recognized by Beilharz (1963).

In order to allocate maternal and sex-linked effects to the statistical parameters estimated by models A and B, it is necessary to establish a biologically accurate model containing the genetic components whose estimates are desired. For this purpose the following models are proposed. The assumptions adhered to are: (1) Mendelian diploid segregation; (2) the *Y*-chromosome is inert. We now let

A_i = the cumulative additive effect of the autosomal genes for line i ,

L_i = the cumulative additive effect of the sex-linked genes for line i ,

M_i = the average maternal effect of line i ,

$S_{ij} = S_{ji}$ = the cumulative non-additive genetic effect specific to the cross of line i and line j (i.e. "specific combining ability" of the cross $i \times j$),

E_{ij} = random effect due to environment and the effects of genetic segregation.

We distinguish four cases which will henceforth be referred to as models 1-4. Letting X_{ij} = progeny mean of the cross of sire line i and dam line j , we have:

1. Homogametic male species, male progeny:

$$X_{ij} = \mu + A_i + L_i + A_j + L_j + M_j + S_{ij} + E_{ij}.$$

2. Homogametic male species, female progeny:

$$X_{ij} = \mu + A_i + L_i + A_j + M_j + S_{ij} + E_{ij}.$$

3. Homogametic female species, male progeny:

$$X_{ij} = \mu + A_i + A_j + M_j + L_j + S_{ij} + E_{ij}.$$

4. Homogametic female species, female progeny:

$$X_{ij} = \mu + A_i + L_i + A_j + M_j + L_j + S_{ij} + E_{ij}.$$

If the p selected lines are considered fixed, we have the restrictions on the parameters,

$$\sum_{i=1}^p A_i = \sum_{i=1}^p M_i = \sum_{i=1}^p L_i = \sum_{j \in Z_i} S_{ij} = \sum_{i \in Z_j} S_{ij} = 0,$$

whereas, if the lines are considered randomly selected inbred lines evolved from a base panmictic population, A_i , L_i , M_i , and S_{ij} are considered as having zero means, and variances σ_A^2 , σ_L^2 , σ_M^2 , and σ_S^2 , respectively, with all random deviates being uncorrelated. In either case the E_{ij} are considered to be mutually uncorrelated with mean zero and variance σ^2 , and in the latter instance, uncorrelated with the other chance variables as well.

(c) *Comparison of the Proposed Models and Model A*

Attention is centred on the direct *meaning* (biological interpretation) of the parameters of model A, which of course is basic to the discussion. The random-effects model will be considered first, since it is somewhat less complex.

TABLE 3
PARAMETRIC RELATIONSHIPS OF MODEL A WITH MODELS 1-4

Parameters (model A)	Sex of Progeny of Homogametic Males		Sex of Progeny of Homogametic Females	
	Male (model 1)	Female (model 2)	Male (model 3)	Female (model 4)
g_j^*	$A_j + L_j$	$A_j + L_j$	A_j	$A_j + L_j$
m_j^*	M_j	$M_j - L_j$	$M_j + L_j$	M_j
r_{ij}^*	0	0	0	0
s_{ij}^*	S_{ij}	S_{ij}	S_{ij}	S_{ij}
<i>Variance Components</i>				
$\sigma_{g^*}^2$	$\sigma_A^2 + \sigma_L^2$	$\sigma_A^2 + \sigma_L^2$	σ_A^2	$\sigma_A^2 + \sigma_L^2$
$\sigma_{m^*}^2$	σ_M^2	$\sigma_M^2 + \sigma_L^2$	$\sigma_M^2 + \sigma_L^2$	σ_M^2
$\sigma_{s^*}^2$	σ_S^2	σ_S^2	σ_S^2	σ_S^2

*Parameter m_j^**

This is the measure of deviation in progeny due to using j as the maternal line, as opposed to using line j as the paternal line. Introducing the operator E^j to denote the *conditional* expectation, *given* line j , it is natural to define

$$m_j^* = E^j(X_{ij}) - E^j(X_{ji}).$$

We shall refer to m_j^* as the *line maternal deviation* which, as we shall see presently, is *not* always the same as the *maternal effect* of line j , namely M_j .

We now interpret m_j^* in terms of the parameters of the proposed model. We illustrate in the case of male progeny of homogametic female species, where

$$X_{ij} = \mu + A_i + A_j + M_j + L_j + S_{ij} + E_{ij},$$

$$E^j(X_{ij}) = \mu + 0 + A_j + M_j + L_j + 0 + 0,$$

$$E^j(X_{ji}) = \mu + A_j + 0 + 0 + 0 + 0 + 0.$$

Hence, in this case,

$$m_j^* = M_j + L_j.$$

The other cases are evolved similarly, and the results are summarized in Table 3.

*Parameter s_{ij}^**

This is the effect of non-additive gene action, and contains the effect of dominance at all loci, as well as epistasis among all combinations of the loci. Note that s_{ij}^* will include epistasis between sex-linked and autosomal genes as well, so that in general the interpretation of non-additive genetic effects also depends upon the sex of the progeny. However, the interpretation of s_{ij}^* is *identical* in model A and the appropriate model 1, 2, 3, or 4.

*Parameter r_{ij}^**

This is the residual reciprocal effect, over and above the contrast between the line maternal deviations. The definition is:

$$r_{ij}^* = \frac{1}{2}[(X_{ij} - E_{ij}) - (X_{ji} - E_{ji})] - \frac{1}{2}(m_j - m_i).$$

The fraction in square brackets is simply a gross contrast between the two reciprocals of the $i \times j$ cross (corrected for segregation and environment peculiar to these crosses), whereas the fraction in parentheses is a correction for the differences between their corresponding *average* advantages of having lines j and i , respectively, as the maternal lines. In every case, the expectation of r_{ij}^* is zero in terms of the parameters of the proposed model, since the model assumes maternal effects which are additive with respect to the direct genetic effects. Thus, the rejection of the hypothesis $H: \sigma_{r^*}^2 = 0$ (a testable hypothesis in Henderson's procedure) might well imply that direct genetic effects and maternal effects are non-additive.

*Parameter g_j^**

This parameter refers to the direct genetic effect of a line, and thus account must be taken of the effect of maternal superiority of the line. Since one-half of the crosses related to a given line have a constant effect of maternal superiority entering into their phenotype, whereas the other half have effects which average zero, the following definition of direct genetic effect of a line is appropriate:

$$g_j^* = \frac{1}{2}E^j(X_{ij} + X_{ji}) - \mu - \frac{1}{2}m_j^*.$$

Given the definition, we can easily evaluate g_j^* in any given case. For example, for female progeny of homogametic male species, we see from Table 3 that

$$m_j^* = M_j - L_j,$$

so that

$$\begin{aligned} g_j^* &= \frac{1}{2}(A_j + M_j + A_j + L_j) - \frac{1}{2}(M_j - L_j) \\ &= A_j + L_j. \end{aligned}$$

Only in this case are the parameters m_j^* and g_j^* of Henderson's model (A) actually correlated. The results for all four cases are summarized in Table 3. In addition, the relationship between the variance components are given.

The Fixed-effects Model

The relationships in the upper half of Table 3 hold with respect to fixed models as well, if care is exercised in the meaning of expectations in this case. The definitions of the effects of Henderson's model (A) must also take into account the parental lines, which are not actually observed in the experiment under consideration. In this case, $r_{ij}^* = 0$, $s_{ij}^* = S_{ij}$ as before. The appropriate definition of the maternal effect of line j for the fixed case is:

$$m_j^* = (1/p) \sum_{i=1}^p [(X_{ij} - E_{ij}) - (X_{ji} - E_{ji})].$$

The absence of parental cross ij ($i = j$) causes no loss of information, however, since it would cancel anyway. Hence, we may use

$$m_j^* = (1/p) \sum_{i \in Z_j} [(X_{ij} - E_{ij}) - (X_{ji} - E_{ji})]$$

as our definition. Taking account of the linear restrictions in the parameters of model A, we see that by successively substituting the right-hand side of model 1-4, the equivalence between the parameters are exactly the same as in the random case.

The situation in the case of g_j^* is slightly more complex. We note that, if all crosses (including parental) are present, we have as the definition,

$$g_j^* = (1/p) \sum_{i=1}^p \left\{ \frac{1}{2} [(X_{ij} - E_{ij}) + (X_{ji} - E_{ji})] - \mu \right\} - \frac{1}{2} m_j^*.$$

The contribution to the sum in the case $i = j$ (parental cross) is easily seen to be $2A_j + KL_j + M_j$ (setting $s_{jj} = 0$ for all j), where $K = 1$ if the progeny are heterogametic, and $K = 2$ if the progeny are homogametic. Thus, we may rewrite g_j^* as follows:

$$g_j^* = (1/p) \left(\sum_{i \in Z_j} \left\{ \frac{1}{2} [(X_{ij} - E_{ij}) + (X_{ji} - E_{ji})] - \mu \right\} + 2A_j + KL_j + M_j \right) - \frac{1}{2} m_j^*.$$

If one now applies models 1-4, the equivalence between the parameters is the same as in the random case.

If models 1-4 are substituted for the X_{ij} in the least-squares estimates of the parameters of model A, and then expectation taken, the same equivalence arises, which would be expected (Eisen 1965).

(d) Comparison of Models 1-4 and Model B

In an exactly analogous manner, the relationship between the parameters of Griffing's model (B) and models 1-4 were derived. No details are included here, but the results are given in Table 4. In every case, general combining ability comparisons are biased by the presence of maternal effects, and in the case of heterogametic offspring, reciprocal effects are a combination of sex-linked effects and maternal effects, whereas in homogametic offspring only maternal effects enter into reciprocal differences.

III. DISCUSSION

It is clear that when data from a modified diallel cross involving only one sex of progeny are analysed, neither model A nor model B provides unconfounded estimates of additive autosomal, additive sex-linked, and maternal effects. Where sex linkage is not involved, as in plants, either model would provide unbiased estimates of additive genetic and maternal effect variances.

TABLE 4
PARAMETRIC RELATIONSHIPS OF MODEL B WITH MODELS 1-4

Parameters (model B)	Sex of Progeny of Homogametic Males		Sex of Progeny of Homogametic Females	
	Male (model 1)	Female (model 2)	Male (model 3)	Female (model 4)
g_j	$A_j + L_j + \frac{1}{2}M_j$	$A_j + \frac{1}{2}L_j + \frac{1}{2}M_j$	$A_j + \frac{1}{2}L_j + \frac{1}{2}M_j$	$A_j + L_j + \frac{1}{2}M_j$
r_{ij}	$\frac{1}{2}(M_j - M_i)$	$\frac{1}{2}(M_j - M_i) - \frac{1}{2}(L_j - L_i)$	$\frac{1}{2}(M_j - M_i) - \frac{1}{2}(L_j - L_i)$	$\frac{1}{2}(M_j - M_i)$
s_{ij}	S_{ij}	S_{ij}	S_{ij}	S_{ij}
<i>Variance Components</i>				
σ_g^2	$\sigma_A^2 + \sigma_L^2 + \frac{1}{4}\sigma_M^2$	$\sigma_A^2 + \frac{1}{4}(\sigma_L^2 + \sigma_M^2)$	$\sigma_A^2 + \frac{1}{4}(\sigma_L^2 + \sigma_M^2)$	$\sigma_A^2 + \sigma_L^2 + \frac{1}{4}\sigma_M^2$
σ_r^2	$\frac{1}{2}\sigma_M^2$	$\frac{1}{2}\sigma_M^2 + \frac{1}{2}\sigma_L^2$	$\frac{1}{2}\sigma_M^2 + \frac{1}{2}\sigma_L^2$	$\frac{1}{2}\sigma_M^2$

In material where sex linkage is involved, and the trait can be measured on progeny of both sexes, the different sex chromosome composition of the sexes could lead to a sex-by-genotype (or cross) interaction. Since $p-1$ crosses would differ between the sexes due to the same sex chromosome and there would be p such sets, the genotype-by-sex interaction component would itself estimate σ_L^2 in the absence of other sources of interaction. If one is willing to assume that no other sources of genotype-by-sex interaction are involved, then unbiased estimates of the mean square or variance components for A , L , and M can be obtained by use of components from both sexes using either model A or B (see Tables 3 and 4).

The problem of estimating these components when considering a trait which can be measured on only one sex, such as egg production, still remains. In the case of female progeny of a male homogametic species (such as poultry), use of terms from both models A and B will yield estimates of the contribution of the additive autosomal, sex-linked, and maternal effects to the mean squares. From model A (Table 3) it is seen that

$$\sigma_{g^*}^2 = \sigma_A^2 + \sigma_L^2,$$

and

$$\sigma_{m^*}^2 = \sigma_M^2 + \sigma_L^2.$$

From model B (Table 4) it is seen that

$$\sigma_g^2 = \sigma_A^2 + \frac{1}{4}\sigma_L^2 + \frac{1}{4}\sigma_M^2.$$

From these values can be derived

$$\sigma_A^2 = \sigma_g^2 - \frac{1}{4}\sigma_m^{2*},$$

$$\sigma_L^2 = \sigma_g^{2*} - \sigma_g^2 + \frac{1}{4}\sigma_m^{2*},$$

and

$$\sigma_M^2 = \sigma_g^2 + \frac{3}{4}\sigma_m^{2*} - \sigma_g^{2*}.$$

The manner in which the components of interest (σ_A^2 , σ_L^2 , and σ_M^2) are confounded in the estimated components (σ_g^2 , σ_g^{2*} , σ_m^{2*} , or σ_r^2) in the other combinations of sex and type of species precludes even the use of parameter estimates from both models for separation of the autosomal, sex-linked, and maternal-effect variances.

Even in the case where possible to do so, the desirability of the estimators based on estimates of parameters obtained from both models may be questioned. For any experiment the total number of observations is fixed. If two independent samples are drawn from each cross and half are used for analysis by model A and half by model B, the number of observations on which the estimates are based for each model will be reduced, while the errors will be uncorrelated. The alternative is to analyse the total data with respect to both models, in which case the estimates would be based on more observations but would be highly correlated. While the undesirable statistical properties of such estimates are recognized, the biases introduced in estimating σ_A^2 , σ_L^2 , and σ_M^2 by this procedure are not clearly understood. On the other hand, this procedure does not require the assumption of the absence of sex-by-genotype interaction above that caused by sex-linked chromosomes.

The need for development of new models specifically designed to isolate unbiased estimates of the components of interest in each sex and each type of species is clearly evident from this study.

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