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Genetic interpretation and analysis of diallel crosses with animals*

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Summary. A genetic framework was developed for the interpretation of statistical parameters estimated from a diallel experiment among a fixed set of lines. These included average direct genetic, average maternal genetic, general combining ability, reciprocal, and line and specific direct and maternal heterotic effects. The genetic model is based on direct and maternal additive and dominance genetic effects as would be expected in animal species. The model assumes that dominance is the underlying basis of heterosis. As an example, litter size at birth was analyzed from a 5 × 5 diallel cross with mice.

Key words: Diallel cross – Maternal effects – Heterosis – Mice

Introduction

The diallel cross is a useful genetic tool for evaluating the performance of lines and breeds in crossbred combinations. Dickerson (1969, 1973) defined various statistical genetic effects that determine mean performance of breeds and crosses. These include direct and maternal average genetic effects and direct and maternal heterosis which can be estimated from a diallel cross experiment. Procedures for estimating these effects by least squares have been extended to an arbitrary set of straightbred and crossbred groups (Dillard et al. 1980; Robison et al. 1980; Alenda et al. 1980; Alenda and Martin 1981). Gregory et al. (1978) listed practical interpretations of these statistical genetic effects. Yet, more effort is needed in building a framework for interpretation of these statistical parameters into genetic components such as additive and dominance effects.

Gardner and Eberhart (1966) extended the diallel models of Henderson (1948) and Griffing (1956) by partitioning direct heterosis effects, with particular emphasis on a fixed set of plant varieties. Vencovsky (1970) derived the genetic interpretation of these heterosis effects.

The objective of the present study is to expand the models of Gardner and Eberhart (1966) and Vencovsky (1970) to include genetic interpretation of diallel crosses among random mating lines or breeds of animals when maternal effects may be important. An example is given of the analysis of litter size in a diallel cross with mice.

Theory

Genetic model

Genetic interpretation of statistical parameters and models described in the next section are essential for formulating breeding plans and understanding the basis of heterosis. The basic genetic model follows that developed by Gardner and Eberhart (1966) with the addition of maternal genetic effects. The model is applicable to a fixed set of lines that have been randomly mated and are in Hardy-Weinberg equilibrium. Although not considered explicitly in the model, the lines may be partially inbred without affecting the assumptions of the model. The model assumes the absence of epistasis, paternal effects, grandmaternal effects and sex-linked effects. Assuming that there are 2 alleles per autosomal locus, let $2\,a_k$ represent the difference between homozygous genotypic values for direct effects at the k^{th} locus, d_k is the dominance direct value of the heterozygote and q_{ik} is the gene frequency of the favorable allele at the k^{th} locus in the i^{th} line, $k = 1, \ldots, n$; $i = 1, \ldots, p$. Analogous terms for maternal effects are $2\,a_k^m$ and d_k^m. Define l_i as the average direct (transmitted) genetic effect $\left(\sum_i l_i = 0\right)$ and m_i as the

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average maternal genetic effect $\left(\sum_i m_i = 0\right)$ of parental line i. Then

$$l_i = \sum_k (2\,q_{ik} - 1)\,a_k - \bar{a} + \sum_k 2\,(q_{ik} - q_{ik}^2)\,d_k - \bar{d} \tag{1}$$

and

$$m_i = \sum_k (2\,q_{ik} - 1)\,a_k^m - \bar{a}^m + \sum_k 2\,(q_{ik} - q_{ik}^2)\,d_k^m - \bar{d}^m \tag{2}$$

where $\bar{a}$, $\bar{d}$, $\bar{a}^m$ and $\bar{d}^m$ are additive direct, dominance direct, additive maternal and dominance maternal contributions to the mean of all parental lines; e.g., $\bar{a} = \frac{1}{p} \sum_i \sum_k (2\,q_{ik} - 1)\,a_k$. Formulas (1) and (2) clearly indicate that average direct and average maternal genetic effects of a line or breed contain dominance effects in addition to additive effects. Dominance direct effects (d_k) could be estimated directly only if selfing of the lines and crosses were possible as, for example, with plant species (Gardner and Eberhart 1966; Eberhart and Gardner 1966). In the future, embryo manipulation such as cloning or germ cell fusion may provide an alternative approach in animal species.

Differences between reciprocal crosses reflect differences in gene frequencies between line i and j in the presence of additive maternal and (or) dominance maternal effects, i.e.,

$$r_{ij} = \sum_k (q_{ik} - q_{jk})\,a_k^m + \sum_k [(q_{ik} - q_{jk}) - (q_{ik}^2 - q_{jk}^2)]\,d_k^m\,, \tag{3}$$

($r_{ij} = -r_{ji}$). Specific reciprocal effects ($r_{ij}^{**} = -r_{ji}^{**}$), defined by subtracting from r_{ij} the average maternal difference between lines i and j, $(m_j - m_i)/2$, have an expectation of zero for maternal effects as defined herein. Significant r_{ij}^{**} may represent specific cytoplasmic effects. Specific reciprocal effects do not contain sex-linked effects (Eisen et al. 1966; Cardonell et al. 1983), contrary to interpretations given by Henderson (1948) and Harvey (1975).

Direct heterosis resulting from the cross of two lines is defined according to the presence of dominance direct effects and the difference in gene frequencies between the lines (Falconer 1981)

$$h_{ij} = \sum_k (q_{ik} - q_{jk})^2\,d_k\,.$$

Gardner and Eberhart (1966) partitioned direct heterosis as follows:

$$h_{ij} = \bar{h} + h_i + h_j + s_{ij} \tag{4}$$

where $\bar{h}$ is overall direct heterosis contributed by the set of lines used in crosses, h_i is direct heterosis of line i as a deviation from overall heterosis $\left(\sum_i h_i = 0\right)$ and s_{ij} is specific combining ability (specific direct heterosis) that occurs in the progeny of lines i and j $\left(\sum_i s_{ij} = \sum_j s_{ij} = 0,\ s_{ij} = s_{ji}\right)$. The term h_i is, apart from a constant, equal to the more usual definition of line heterosis used in animal breeding literature ($\bar{h}_i$), deviated from $\bar{h}$, i.e., $h_i = (\bar{h}_i - \bar{h})\,(p-1)/(p-2)$ where $\bar{h}_i = \sum_{\substack{j \\ (j \neq i)}} h_{ij}/(p-1)$ and $\bar{h} = \sum_{i<j}\sum h_{ij}/[p\,(p-1)/2]$.

Casas and Wellhausen (1968) showed that (4) can be rearranged to give

$$h_{ij} = z_i + z_j - 2\,w_{ij} \tag{5}$$

where $z_i = \sum_k \gamma_{ik}^2\,d_k$, $w_{ij} = \sum_k \gamma_{ik}\,\gamma_{jk}\,d_k$, $\gamma_{ik} = q_{ik} - \bar{q}_k$, and $\bar{q}_k = \frac{1}{p} \sum_i q_{ik}$.

Vencovsky (1970) provided considerable insight into genetic interpretation of $\bar{h}$, h_i and s_{ij} by deriving z_i and w_{ij} in terms of parental line and crossbred means, as reviewed by Hallauer and Miranda (1981).

Overall direct heterosis can be rewritten as $\bar{h} = [2\,p/(p-1)]\,\bar{z}$ where $\bar{z} = \frac{1}{p} \sum_i z_i = \sum_k \sigma_{q_k}^2\,d_k$, and $\sigma_{q_k}^2$ is the variance of gene frequency at the k^th^ locus among all lines. From the relationships derived in (5), line direct heterosis is given by

$$\begin{aligned} h_i &= [p/(p-2)]\,[z_i - \bar{z}] \\ &= [p/(p-2)]\left[\sum_k \gamma_{ik}^2\,d_k - \sum_k \sigma_{q_k}^2\,d_k\right]. \end{aligned} \tag{6}$$

Therefore, when $z_i = 0$, h_i will be the largest negative value and $\bar{h}_i$ the smallest positive value among the set of lines used in the diallel because $q_{ik} = \bar{q}_k$, provided $d_k > 0$. Line direct heterosis will be relatively high for line i when $\bar{h}_i > 0$, $z_i > \bar{z}$ or $h_i > \bar{h}$, a situation arising when a line has many loci at high gene frequency, or at low gene frequency or a combination of loci at high and low gene frequency (Vencovsky 1970). In contrast, a relatively low degree of line heterosis is present if z_i is close to zero, in which case h_i will be one of the largest negative values and $\bar{h}_i$ will be small. This result would be expected if most loci of the line are close to the mean gene frequency. Since h_i, z_i and $\bar{h}_i$ are exactly positively linearly related, only one of these statistics needs to be presented. The advantage of using $\bar{h}_i$ is that it is presently commonly used in animal breeding literature. Use of h_i would be appropriate in evaluating the relative contribution of line heterosis to heterosis (4) and to general combining ability (7). The term z_i detects the degree of departure of q_{ik} from $\bar{q}_k$.

General combining ability is the average performance of lines in crosses (Sprague and Tatum 1942). Gardner and Eberhart (1966) derived the general relationship between general combining ability effects and average line effects for noninbred lines. General combining ability of line i, adjusted for maternal effects, is given by

$$g_i = (1/2)\, l_i + h_i, \quad \Big(\sum_i g_i = 0\Big), \tag{7}$$

where l_i and h_i are in formulas (1) and (6), respectively. Therefore, the magnitude of g_i is determined by additive direct effects, dominance direct effects, the deviation of gene frequency of the line from mean gene frequency at each locus, and the number of lines in the diallel.

Applying the same notions for specific direct heterosis yields

$$s_{ij} = [2/(p-2)]\,\{[p/(p-1)]\,\bar{z} - z_i - z_j\} - 2\,w_{ij}\,.$$

Specific heterosis is exactly negatively related to w_{ij} only for large p, in which case $s_{ij} = -2\,w_{ij}$. For this situation, the highest absolute values of s_{ij} occur when gene frequency of both lines diverge the most from mean gene frequency at loci exhibiting favorable dominance direct effects. The numerical value of w_{ij} will be negative when γ_{ik} and γ_{jk} are of opposite sign and positive when they have the same sign. For small values of p, usually encountered in diallel crosses with animals, the negative relationship between s_{ij} and w_{ij} still holds, but the deviations from regression can be large. Therefore, it is more reliable to use w_{ij} than s_{ij} for interpreting the degree of divergence in gene frequency between two lines.

Finally, although not possible to estimate from a diallel experiment, maternal heterosis, conceptually, can be partitioned in a manner similar to direct heterosis as follows:

$$h^m_{ij} = \bar{h}^m + h^m_i + h^m_j + s^m_{ij} = z^m_i + z^m_j - 2\,w^m_{ij}$$

where $\bar{h}^m$ = overall maternal heterosis, h^m_i = line maternal heterosis, s^m_{ij} = specific maternal heterosis,

$$z^m_i = \sum_k \gamma^2_{ik}\, d^m_k \quad \text{and} \quad w^m_{ij} = \sum_k \gamma_{ik}\, \gamma_{jk}\, d^m_k\,.$$

These estimates of maternal heterosis can be obtained from F_2 and backcross data.

Statistical model

The model representing the mean of a parental line or cross is

$$\bar{y}_{ij} = \bar{y}_a + (l_i + l_j)/2 + m_j + \delta\,(h_{ij} + r^{**}_{ij}) \tag{8}$$

where

$\bar{y}_{ij}$ = mean performance of offspring of sire line i mated to dam line j (i, j = 1, …, p), $\delta = 0$ for parental line progeny (i = j), $\delta = 1$ for crossbred progeny (i ≠ j),

$\bar{y}_a$ = mean of parental lines,

$m_j = \bar{y}_{.j} - \bar{y}_{j.}$,

$\bar{y}_{j.}\,(\bar{y}_{.j})$ = mean of sire (dam) line j including the parental line,

$l_i = \bar{y}_{ii} - \bar{y}_a - m_i$,

$h_{ij} = (\bar{y}_{ij} + \bar{y}_{ji})/2 - (\bar{y}_{ii} + \bar{y}_{jj})/2$,

$r^{**}_{ij} = r_{ij} - (m_j - m_i)/2$

and

$r_{ij} = (\bar{y}_{ij} - \bar{y}_{ji})/2$.

The model describing the diallel analysis excluding parental lines (Henderson 1948; Eisen et al. 1966) may be derived from (8) by letting $\delta = 1$ and using identities (4), (7) and $\bar{h} = \bar{y}_c - \bar{y}_a$ where $\bar{y}_c$ is the crossbred mean, which yields

$$\bar{y}_{ij} = \bar{y}_c + g_i + g_j + m_j + s_{ij} + r^{**}_{ij}\,. \tag{9}$$

Least squares formulas for general and specific combining ability effects, adjusted for maternal effects (Henderson 1948; Eisen et al. 1966), are given by

$$g_i = \frac{p-1}{p\,(p-2)}\,[(p-1)\,\bar{y}^*_{i.} + \bar{y}^*_{.i} - p\,\bar{y}_c] \quad \text{and}$$

$$s_{ij} = (\bar{y}_{ij} + \bar{y}_{ji})/2 - \frac{p-1}{2\,(p-2)}\,(\bar{y}^*_{i.} + \bar{y}^*_{.i} + \bar{y}^*_{j.} + \bar{y}^*_{.j}) + \frac{p}{p-2}\,\bar{y}_c$$

where $\bar{y}^*_{i.}\,(\bar{y}^*_{.i})$ is the mean of sire (dam) line i averaged over crosses with all other lines, excluding the parental lines.

Analyses of variance procedures for models based on formulas (8) and (9) were presented by Gardner and Eberhart (1966) and Harvey (1975).

The mean of sire line i, inclusive of the parental line, is

$$\bar{y}_{i.} = \bar{y}_a + (1/2)\, l_i + \bar{h}_i\,(p-1)/p,$$

and the mean for the corresponding dam line is

$$\bar{y}_{.i} = \bar{y}_{i.} + m_i\,.$$

Gregory et al. (1978) suggested that the best estimate of the contribution of a line used as a sire and dam in crosses is $\bar{y}^*_i = (\bar{y}^*_{i.} + \bar{y}^*_{.i})/2$. Expectation of this mean is given by

$$\begin{aligned}\bar{y}^*_i &= \bar{y}_a + (l_i + m_i)\,(p-2)/[2\,(p-1)] + \bar{h}_i\\ &= \bar{y}_c + (2\,g_i + m_i)\,(p-2)/[2\,(p-1)]\,.\end{aligned} \tag{10}$$

Substituting the genetic effects from (1), (2) and (5) into $\bar{y}_{i.}$, $\bar{y}_{.i}$ and $\bar{y}^*_i$ illustrates the contributions made by additive and dominance effects for both direct and maternal sources of variability.

Least squares estimates of z_i and w_{ij} given by Vencovsky (1970) have to be adjusted for maternal effects as follows:

$$z_i = \frac{1}{2p}\,[(p-1)\,(\bar{y}^*_{i.} + \bar{y}^*_{.i} - \bar{y}_c) - (p-2)\,\bar{y}_{ii} - \bar{y}_a]\,,$$

$$w_{ij} = -\frac{1}{4}(\bar{y}_{ij} + \bar{y}_{ji}) + \frac{(p-1)}{4p}(\bar{y}^*_{i.} + \bar{y}^*_{.i} + \bar{y}^*_{j.} + \bar{y}^*_{.j}) + \frac{1}{2p}(\bar{y}_{ii} + \bar{y}_{jj}) - \frac{(p-1)}{2p}\bar{y}_c - \frac{1}{2p}\bar{y}_a .$$

Estimates of each effect can be obtained by forming contrasts among the appropriate least squares means. Although the number of linear contrasts made using the least squares means exceeds the number of degrees of freedom, the contrasts are developed a priori to provide insight into the importance of average direct, average maternal and direct heterotic effects.

Application

A diallel experiment with five lines of mice will be used as an illustration. The lines included L^+, selected for large litter size; W^+, selected for large 6-week body weight; L^-W^+, selected for small litter size and large 6-week body weight; L^+W^-, selected for large litter size and small 6-week body weight; and K, an unselected control (Eisen 1978). Selection was practiced for 23 generations and subsequently relaxed for six generations prior to crossing the lines. Line inbreeding coefficients ranged from 20 to 28%. Dams representing the five lines and 20 reciprocal F_1 crosses were mated to a sixth line of males, and data were collected for litter size at birth (Table 1).

Table 1. Mean litter size at birth in a 5 × 5 diallel[a]

Dam / Sire	L^+	W^+	L^-W^+	K	L^+W^-	$\bar{y}^*_{i.}$	$\bar{y}_{i.}$
L^+	19.0	19.5	16.0	16.8	17.7	17.5	17.9
W^+	17.3	15.3	14.4	14.2	16.9	15.7	15.6
L^-W^+	15.7	15.3	10.9	12.3	14.1	14.4	13.7
K	15.9	15.4	12.7	12.5	14.2	14.6	14.1
L^+W^-	17.5	16.2	15.5	14.8	16.3	16.0	16.1
$\bar{y}^*_{.i}$	16.6	16.6	14.7	14.5	15.7	$\bar{y}_c =$	15.6
$\bar{y}_{.i}$	17.1	16.3	13.9	14.1	15.8	$\bar{y}_a =$	14.8
$\bar{y}^*_i$	17.1	16.2	14.6	14.6	15.9		

[a] Sample sizes ranged, from 37 to 51 and standard errors of subclass means ranged from 0.53 to 0.62

Table 2. Least squares estimates of average direct genetic effects (l_i), average maternal genetic effects (m_i) and general combining ability (g_i) for litter size

Line	l_i	m_i	g_i
L^+	4.97[a]	− 0.73[a]	2.27[a]
W^+	− 0.26[b]	0.74[c]	0.35[b]
L^-W^+	− 4.16[c]	0.27[bc]	− 1.62[c]
K	− 2.27[d]	− 0.03[abc]	− 1.43[c]
L^+W^-	1.71[e]	− 0.24[ab]	0.44[b]
SE[f]	0.61	0.32	0.26

[a, b, c, d, e] Column means under the same heading with no letters in common are significantly different at $P < 0.05$

[f] Approximate standard error of least squares estimates

Line differences in litter size (diagonal means in Table 1) reflect the intended direction of the selection criteria for L^+, L^-W^+ and L^+W^- and the positive genetic correlation between litter size and adult body weight for W^+. Total direct response in L^+ and correlated response in W^+, L^-W^+ and L^+W^- for litter size were partitioned into average direct and average maternal genetic effects (Table 2). The major selection response occurred for direct genetic effects. Line L^+ had the largest l_i followed by L^+W^- and then by W^+, all of which exceeded the control line. A negative response was observed in l_i for line L^-W^+. For average maternal genetic effects, the most striking difference occurred between L^+ and W^+ (Table 2). Although not significantly different from the control line, the m_i value for W^+ was significantly larger than that for L^+.

The conclusion drawn from these estimates is that selection in these lines has caused major changes in gene frequency at loci having direct genetic effects on litter size. These genetic differences among lines may be due to both additive and dominance effects, but the present analysis does not permit distinction between them. Maternal genetic changes due to selection have been lower in magnitude than for direct effects. The explanation for this may be twofold. First, nuclear genes influencing maternal effects on litter size may have smaller effects. Second, the covariance between direct and maternal genetic effects for litter size may not be particularly large so that loci affecting primarily maternal influences have not shifted much in gene frequency.

General combining ability provides an estimate of the best combination of direct genetic effects in crosses, and includes average direct genetic and line heterotic effects (formulas 1, 6 and 7). Line L^+ had the highest g_i for litter size, followed by W^+ and L^+W^- (Table 2). The latter two lines had g_i values which were larger than those for lines L^-W^+ and K. Ranking of the lines for g_i was identical to that for $\bar{y}^*_i$ (Table 1), whose expectation is a function of g_i and m_i (formula 10). Gregory et al. (1978) termed $\bar{y}^*_i$ as the net breed effect in crosses, and suggested that it be used as a criterion for estimating the relative utility of a population for rotational crossing or forming a synthetic. The present results support this view.

Line direct heterosis for litter size is presented in Table 3. Overall direct heterosis was highly significant. All populations showed some degree of line direct heterosis, although $\bar{h}_i$ for L^+W^- was not significant.

Table 3. Line direct heterosis for litter size

Line	$\bar{h}_i$	h_i	z_i
L^+	0.67 ± 0.37*	-0.22 ± 0.33	0.20 ± 0.22
W^+	1.19 ± 0.38**	0.48 ± 0.33	0.62 ± 0.23**
L^-W^+	1.18 ± 0.40**	0.46 ± 0.34	0.61 ± 0.24**
K	0.61 ± 0.37*	-0.30 ± 0.32	0.15 ± 0.22
L^+W^-	0.52 ± 0.38	-0.42 ± 0.33	0.08 ± 0.23
$\bar{h}$[a]	0.83 ± 0.29**		

* $P<0.10$; ** $P<0.01$

[a] Overall heterosis

Values of z_i suggest that W^+ and L^-W^+ have gene frequencies that diverged considerably from mean gene frequency, L^+ and K diverged moderately, and L^+W^- had gene frequencies that were close to $\bar{q}_k$. Based on the magnitude of line heterosis, W^+ and L^-W^+ would be expected to contribute the most to direct heterosis of a cross (h_{ij}). This expectation was realized and, in fact, $W^+ \times L^-W^+$ exhibited the highest percent direct heterosis (Table 4).

Several points are evident from ranking of lines for direct heterosis in Table 4. Although litter size in mice is expected to be a heterotic trait because it is associated with fitness, not all crosses exhibited heterosis. Based on h_{ij}, there is a suggestion that the ten crosses represent three degrees of heterosis: large (crosses 1 to 3), moderate (crosses 4 to 8) and negligible (crosses 9 to 10). However, the standard errors of h_{ij} were too large to draw an unequivocal conclusion. The crosses showing no heterosis may be examples of lines where the gene frequency for particular components of litter size that show dominance have not been modified by selection or, alternatively, the components of litter size that have been modified are mainly additive.

Specific combining ability effects do not have to be large for a cross to exhibit heterosis, as exemplified by $W^+ \times L^-W^+$ where positive line heterosis (h_i) for W^+ and L^-W^+ contributed most of the heterosis to h_{ij}, and s_{ij} was negligible. In contrast, heterosis in $L^+W^- \times L^-W^+$ was primarily due to s_{ij} because line heterosis values for L^+W^- and L^-W^+ were of approximately equal magnitude but opposite in sign.

As noted in the previous section, inferences regarding the magnitude of gene frequency differences between lines and whether or not the deviations, γ_{ik} and γ_{jk}, for lines i and j are of the same or opposite sign should be based on w_{ij} and not on s_{ij} unless p is large. This conclusion is supported by the correlation of $-.72$ ($P < .05$) between s_{ij} and w_{ij} for litter size in the present diallel, indicating that only about fifty percent of the variation in w_{ij} was accounted for by s_{ij}. Relatively large negative values for w_{ij} in crosses 1 to 3 (Table 4) indicate that for loci contributing dominance effects to litter size the gene frequency differences between parental lines were large and γ_{ik} and γ_{jk} were of opposite sign. Smaller negative values for w_{ij} in crosses 4 to 8 imply divergence in gene frequency and (or) smaller contribution of dominance at loci contributing to line differences. Positive w_{ij} values for crosses 9 and 10 suggest that the lines involved in these two crosses diverged in gene frequency in the same direction, i.e., γ_{ik} and γ_{jk} were either both negative or both positive.

Reciprocal effects (r_{ij}) were significant for reciprocal crosses $L^+ \times W^+$ ($P < .01$), $L^-W^+ \times L^+W^-$ ($P < .10$) and $W^+ \times K$ ($P < .10$). In the case of $L^+ \times W^+$, the W^+ dams had a higher frequency of desirable alleles that provided a maternal genotype superior to L^+ (formula 3). This enabled F_1 female progeny reared by W^+ mothers to produce a larger litter than females reared by L^+ dams. Similary, $L^- W^+$ dams were supe-

Table 4. Estimates of h_{ij}, s_{ij}, w_{ij}, r_{ij} and r^{**}_{ij}

Cross[a]	h_{ij}	$h_{ij}\%$[b]	s_{ij}	w_{ij}	r_{ij}	r^{**}_{ij}
1. $W^+ \times L^-W^+$	1.78***	13.6	0.01	-0.28*	-0.45	-0.21
2. $L^+ \times W^+$	1.28**	7.5	0.19	-0.23	1.09***	0.36
3. $L^-W^+ \times L^+W^-$	1.22**	9.0	0.35	-0.27	-0.73*	-0.48
4. $W^+ \times K$	0.91*	6.5	-0.10	-0.07	-0.64*	-0.26
5. $L^+ \times L^-W^+$	0.86	5.8	-0.21	-0.03	0.16	-0.34
6. $L^-W^+ \times K$	0.84	7.1	-0.15	-0.04	-0.22	-0.07
7. $W^+ \times L^+W^-$	0.79	5.0	-0.10	-0.05	0.33	0.82***
8. $L^+ \times K$	0.58	3.7	0.26	-0.11	0.48	0.13
9. $K \times L^+W^-$	0.11	0.7	-0.01	0.06	-0.29	-0.19
10. $L^+ \times L^+W^-$	-0.04	-0.2	-0.24	0.16	0.09	-0.16
SE[c]	0.56	–	0.28	0.17	0.39	0.31

* $P<0.10$; ** $P<0.05$; *** $P<0.01$

[a] Includes reciprocals

[b] Percent of midparent

[c] Approximate standard error of least squares estimate

rior to L^+W^- dams and W^+ dams were superior to K dams. The only significant specific reciprocal effects (r_{ij}^{**}) encountered were for $W^+ \times L^+W^-$. The positive value suggests that L^+W^- dams may contribute a desirable cytoplasmic effect relative to W^+ dams. This may involve a specific interaction since L^+W^- dams did not confer positive specific reciprocal effects involving the other lines.

Discussion

Crossbreeding has been a central issue in formulating animal breeding plans in recent years (Moav 1966; Dickerson 1969; Hill 1971). Crossbreeding experiments with livestock often have lacked clear genetic interpretation of statistical parameters. To mention just one crossbreeding study with beef cattle, the term for line direct heterosis was incorrectly identified as general combining ability (Stewart et al. 1980). These two terms have distinct genetic expectations (formulas 6 and 7) which could lead to confusion in interpretation of genetic effects.

To overcome many of these difficulties, the diallel analysis developed by Gardner and Eberhart (1966) with extended interpretations of direct heterosis (Vencovsky 1970) was generalized to include maternal genetic effects. Direct heterosis effects were based on a dominance model that assumes negligible epistatic effects. Partitioning of maternal heterosis into overall, line and specific effects was developed for advanced generations of crossing.

The assumption of no epistasis may be tested statistically (Gardner and Eberhart 1966). McGloughlin (1980) reported that a dominance model was adequate to explain heterotic effects for reproductive traits of mice, but F_2 crosses were not available to test for epistasis. Sheridan (1981) reviewed several experiments where epistasis was reported to be important. For example, Sheridan (1980) found epistatic heterosis for egg production in crosses between White Leghorn and Australorp chickens. Statistical genetic models have been developed to estimate epistatic effects in animal populations (Kinghorn 1980, 1982).

Sex-linkage has been assumed to be zero. Sex-linked effects have not been found to be an important component of quantitative traits in mammals, but are known to be important in poultry (Gowe and Fairfull 1982). Eisen et al. (1966) have dealt with estimating sex-linked effects in a diallel cross among inbred lines. Carbonell et al. (1983) extended the model of Eberhart and Gardner (1966) to include sex-linked effects.

The diallel cross with mice illustrates application of the model to analysis of a highly heterotic trait. Lines with a well-defined history of selection were evaluated in terms of correlated responses in average direct and average maternal genetic effects. Potential merit of specific lines in crossbreeding programs was also demonstrated. Partitioning of direct heterosis for litter size showed the genetic impact of line and specific heterosis in each cross. The data were used to show that genetic interpretation of dominance effects are clarified by using the parameter estimates z_i and w_{ij} as opposed to h_i and s_{ij}.

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