HETEROSIS, COMBINING ABILITY, AND MATERNAL EFFECTS IN MICE[1]

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The results of most crossbreeding work have in general shown an advantage in the performance of crosses over that of their parents; however, the literature concerning the general and specific combining ability of lines is not extensive. Combining ability as used by animal and plant breeders is divided into general and specific combining ability. General combining ability is a measure of the average performance of a line in hybrid combination, while specific combining ability refers to specific crosses that do better or worse than would be expected based on the average performance of the lines involved.

Henderson (1948) developed a mathematical model for estimating and testing general and specific combining ability, maternal, and sex linked effects in crosses of lines involving multiple classification with disproportionate subclass numbers.

The test reported here was devised to study the degree of heterosis, general and specific combining ability, maternal, and sex linked effects in crosses of four lines of mice.

Materials and Methods

Four lines of mice were available for this study. Line *W* was an outbred Webster strain; lines *M* and *F* were slightly inbred strains developed at this laboratory from two commercial stocks and carried approximately 15 percent inbreeding. The fourth line designated as *C* was highly inbred and was maintained at the laboratory by brother-sister mating. This line was obtained originally from the Roscoe Jackson Laboratories. Breeders were selected at random; no artificial selection was applied to these lines for any trait.

The females were first mated at 75 days of age. First litters only were used for this study. At 21 days, the litters were weaned, weighed, and numbered. The sexes were separated, and 10 mice of each sex were fed in a cage until they were 45 days of age, when individual weights were obtained. A standard laboratory ration was fed.

All possible crosses and reciprocals were made among the four lines. Data were collected on 1824 individuals from 312 litters, and at least 5 litters were produced for each of the 16 possible subclasses.

The model used in the analysis was the one formulated by Henderson (1948), and extended by Harvey (1960). The model for 21 and 45 day weights was as follows:

$$y_{ijklm} = u + s_i + a_j + p_{1k} + g_{2k} + g_{2l} + m_{2l} + c_{2kl} + r_{2kl} + b(X - \bar{X}) + e_{ijklm}$$

where

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y_{ijklm} = the average 21 or 45 day weight for the m^{th} individual produced by mating a dam of the l^{th} line to a sire of the k^{th} line to produce the j^{th} type of cross for the i^{th} sex. The subscript j indicates whether the offspring obtained is a linebred ($j=1$) or a single cross ($j=2$),

u = the general mean when all subclass frequencies are equal,

s_i = the effect of the i^{th} sex,

a_j = the effect of the j^{th} type of cross,

p_{1k} = the effect of the k^{th} linebred within the linebreds,

g_{2k} = the general combining ability effect from the k^{th} line of sire,

g_{2l} = the general combining ability effect from the l^{th} line of dam,

m_{2l} = the maternal effect for the l^{th} line of dam,

c_{2kl} = the specific combining ability effect for the kl or lk cross,

r_{2kl} = the sex linked or reciprocal effects,

b = the partial regression of number of mice weaned per litter on weight (21 or 45 days),

X = the number of mice weaned per litter, and

e_{ijklm} = error that is particular to all individuals within sex-litter subclass.

The model used to express the number of mice at birth and 21 days was as follows:

$y_{jklm} = u+a_j+p_{1k}+g_{2k}+g_{2l}+m_{2l}+c_{2kl}+r_{2kl}+e_{jklm}$ where the symbols are as defined before.

A conventional least square analysis was used to estimate all constants and all tests of significance where made under the assumption of fixed line effects.

Results and Discussion

Weights

The analysis of variance for 21 and 45 day weight are shown in Table 1.

A highly significant difference between sexes in favor of the males was observed for weights at both ages. This is in agreement with other reports; Carmon (1960), using two of the same lines of mice, and in rats, King (1915) and Kidwell *et al.* (1960).

Heterosis measured as a comparison between the linebreds and crossbreds was highly significant for weight at both 21 and 45 days of age. Kidwell *et al.* (1960) found that heterosis in rats was significant at 70 days but not at 28 days. Other evidence that heterosis effects increased with increasing age has been reported by Livesay (1930) working with rats and in swine by Dickerson *et al.* (1946) and Chambers and Whatley (1951). A comparison of the least square means for the single crosses and the average of the two parental lines, Table 2, shows that the deviations of the single crosses from the average of the linebreds were greater for some crosses in this study at 45 days of age than at 21 days. The *MF* cross was not significantly greater than the average of the *M* and *F* linebreds at 21 days but was significant at 45 days of age. The average heterosis for crosses involving line *W* was 1·56 grams at 21 days of age and 2·84 grams at 45 days of age. The average values for lines *M*, *F*, and *C* were 1·07, 1·18, and 1·77

Table 1. *Analysis of Variance for 21 Day Weight and 45 Day Weight*

Source	df	Mean Squares 21 Days	45 Days
Sex	1	48·62**	5250·31**
Heterosis	1	473·12**	1666·01**
Linebreds	3	484·44**	3653·48**
Gen. Combining Ability	3	34·51**	89·56**
Spec. Combining Ability	2	4·16	2·50
Maternal Effects	3	101·53**	185·94**
Sex Linked Effects	3	33·14**	116·70**
Error	1806	3·82	9·40

** Significant at ·01 level of probability.

grams respectively for 21 days of age and 2·22, 2·21 and 3·30 grams for 45 days of age. Thus, line *C* performed the best in crosses and line *M* performed the poorest. Line *C* was the poorest performing linebred being 1·68 and 4·69 grams below the mean at

Table 2. *Heterosis Exhibited by Each Cross Separately*

Cross	21 Day Weight (Grams) Mean Linebreds	Mean Crosses	Diff.	45 Day Weight (Grams) Mean Linebreds	Mean Crosses	Diff.
WM	9·75	10·97	1·22**	23·41	26·22	2·81**
WF	8·85	9·91	1·06**	21·46	23·44	1·98**
WC	8·25	10·65	2·40**	19·74	23·47	3·73**
MF	9·11	9·87	0·76	21·14	22·31	1·17**
MC	8·51	9·75	1·23**	19·42	22·09	2·67**
FC	7·61	9·31	1·70**	17·47	20·96	3·49**
Overall	8·68	10·07	1·39**	20·44	23·08	2·64

** Significant at ·01 level of probability.

21 and 45 days of age, Table 3. Line *M* was the better performing inbred. This agrees with Kidwell *et al.* (1960) who reported, that in crosses of inbred lines of rats, the best performing line performed the poorest in crosses.

General combining ability effects were highly significant for weights at both ages, Table 1. Eaton *et al.* (1950) found that general combining ability effects were important for mouse weights at 15 and 45 days of age. Kidwell *et al.* (1960) using crosses of inbred lines of rats found that general combining ability was significant at 28 days but not at 70 days. Hetzer *et al.* (1961) studied combining ability in crosses of lines of swine, and reported that general combining ability was significant for litter weight at 56 days but not for pig weight at 21 or 56 days of age.

Line differences in general combining ability effects between the best and poorest lines were 1·42 grams for 21 day weight and 2·72 grams for 45 day weight, Table 3.

Specific combining ability effects were non-significant for weight at either age. In a study of 72 crosses of inbred mice, Eaton *et al.* (1950) found that specific effects were important but not significant for viability, total litter weight, and mouse weight. Hetzer *et al.* (1961) failed to find specific effects for litter size or weights at birth, 21, or 56 days of age in crosses of lines of swine.

Highly significant maternal effects were found for weight at both 21 and 45 days of age. This agrees with the report of Eaton *et al.* (1950), Chai (1956) and Marshak (1936). Cox *et al.* (1959) using a cross nursing technique with mice found that maternal effects accounted for 81·2 percent of the variance for 12 day weight. Henderson (1949) found no maternal effects in crosses of swine; however, Hetzer *et al.* (1961) reported significant maternal effects for litter weight and pig weight at 56 and 140 days of age. Magee and Hazel (1959) studied maternal effects in litters produced by a crossbred dam and an inbred sire. They found that maternal effects of the lines were small for 154 day weights.

The ranges in line of dam effects were 2·93 grams for 21 day weight and 3·64 grams for 45 day weight. Line *C* had the poorest maternal ability for weights at both ages. This line carried the highest inbreeding coefficient of the four lines, and since inbreeding in swine has been shown to have a marked effect on female productivity, Wright (1922), Dickerson (1947) and Comstock and Winters (1944), the poor maternal ability of this line could be attributed to the high level of inbreeding. Line *M*, which was a slightly inbred line, had the best maternal ability. Since 45 day weight is made up in part of 21 day weight, the existence of maternal effects for 45 day weight could be a reflection of maternal effects on 21 day weight. This condition is supported in part by the positive correlation ($r=0{\cdot}93$) found between the constants for maternal effects at 21 and 45 day weight.

A comparison of the maternal effects as measured in the linebreds with those in the crossbreds will indicate if there are non-additive effects operating within the line. This comparison is possible since the additive genetic effects as estimated from crosses provided an unbiased estimate of genic effects for crosses and linebreds. A comparison of $2\hat{g}_{2k}+\hat{m}_{2l}$ with $\hat{p}_{1k}$ for each line was non-significant. The correlations between the observed and expected constants were 0·68 and 0·92 for 21 day and 45 day weights, respectively. This indicates that the lines do not rank differently with respect to maternal effects when the dams are rearing either crossbred or linebred litters. Kidwell *et al.* (1960) found that there was an interaction between maternal effects and mating systems for 28 day weight but not for 70 day weight.

Sex linked or reciprocal effects were highly significant for weight at 21 and 45 days. Henderson (1949) and Hetzer *et al.* (1961) found no evidence of sex linkage in swine.

Table 3. *Least Square Constants for Weight and Litter Size*

Source	Weight 21 Day	Weight 45 Day	Litter Size Birth	Litter Size 21 Day
$\hat{u}$	9·38	21·76	7·02	6·29
Sex Effects $\hat{s}_i$				
1 (Males)	·17	1·73	..	..
2 (Females)	— ·17	— 1·73	..	..
Heterosis Effects $\hat{a}_j$				
1	— ·70	— 1·32	— ·06	·11
2	·70	1·32	·06	·11
Purebred Effects $\hat{p}_{1k}$				
W	·80	3·29	·83	·50
M	1·35	2·65	·11	·31
F	— ·48	— 1·25	·01	·30
C	—1·68	— 4·69	·95	—1·11
Genic Value $\hat{g}_{2k}$				
W	·78	1·98	— ·21	·41
M	— ·64	— ·51	·03	— ·16
F	— ·52	— ·74	·09	— ·33
C	·38	— ·73	·10	·08
Maternal Effects $\hat{m}_{2l}$				
W	— ·26	— ·08	·51	·37
M	1·64	2·38	·69	·80
F	— ·10	— 1·05	—1·40	— ·98
C	—1·29	— 1·26	·20	— ·20

Source	Weight 21 Day	Weight 45 Day	Litter Size Birth	Litter Size 21 Day
Crossbred Effects $\hat{c}_{2kl}$				
WM	·06	·51	—·05	—·34
WF	— ·25	— ·32	—·07	·52
WC	·18	— ·20	·12	—·17
MF	·18	— ·20	·12	—·17
MC	— ·25	— ·32	—·07	·52
FC	·06	·51	—·05	—·34
Reciprocal Crosses $\hat{r}_{2kl}$				
WM	·49	·37	—·34	—·18
WF	—1·08	—1·80	·77	—·39
WC	·59	1·43	—·43	·57
MW	— ·49	— ·37	·34	·18
MF	·87	1·46	—·45	·42
MC	— ·38	—1·09	·11	—·60
FW	1·08	1·80	—·77	·39
FM	— ·87	—1·46	—·11	—·42
FC	— ·21	— ·34	·88	·03
CW	— ·59	—1·43	·43	—·57
CM	·38	1·09	·45	·60
CF	·21	·34	—·88	—·03
$\hat{b}$	— ·52	— ·32		

LITTER TRAITS

The analysis of variance for number of mice born and number weaned are shown in Table 4, and the least square constants are presented in Table 3. The only differences observed were differences among the linebreds. The range in purebred line effect was −·95 to ·83 mice per litter for birth and −1·11 to ·50 mice per litter at 21 days of age. The *C* line had the smallest litters while the *W* line had the largest litters. This difference may be a reflection of the inbreeding carried by these lines. Hetzer *et al.* (1961) found no maternal, general, or specific combining ability effects for litter size at birth, 21, and 56 days of age with crosses of lines of swine; however, Chambers and Whatley (1951) reported heterosis for litter size in single crosses of inbred lines of swine.

Table 4. *Analysis of Variance for Litter Size*

Source	df	Mean Square	
		No. Born	No. Weaned
Heterosis	1	0·47	1·85
Linebreds	3	31·83**	31·83**
Gen. Combining Ability	3	0·15	1·03
Spec. Combining Ability	2	0·24	2·66
Maternal Effects	3	6·22	4·70
Sex Linked Effects	3	2·41	3·30
Error	296	5·05	4·99

** Significant at ·01 level of probability.

SUMMARY AND CONCLUSIONS

These data are in general agreement with those found with other mammalian species. Maternal effects for weights were demonstrated with these data and have also been reported in other work with mice and rats; however, maternal effects have been lacking in studies with swine.

Heterosis was evident for weights at 21 and 45 days, but was not present for litter size. General combining ability and sex linked effects were highly significant for weights but not for litter size. There was no evidence of an interaction between maternal effects and mating systems.

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