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Diallel Cross Analysis of Body Weight in Subspecies of Mice

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Abstract: A complete 4 × 4 diallel cross of CF#1 (C), C57BL/6NCrj (B) C3H/HeNCrj (H) and Yonakuni wild mice (Y, *Mus musculus molossinus yonakuni*) has been conducted to estimate the effects of sex, degree of heterosis, general combining ability (gca), specific combining ability (sca), maternal ability, and reciprocal cross on body weight at 1(Wk1), 3 (Wk3), 6 (Wk6) and 10 (Wk10) weeks of age. A least squares analysis was performed on 828 mice and all sources of variation showed significant effects (P<0.01) on body weight but not sex at Wk1 (P>0.05). Males were heavier than females (P<0.01) at Wk3, Wk6 and Wk10. C and Y were the heaviest and lightest in body weight, whereas H and B were intermediate. Differences in body weight were observed between linebred and linecross at all ages studied: 6.57%, 10.22%, 8.70% and 5.89% heterosis for the respective ages. The degree of gca and maternal effects can be ranked as C>H>B>Y. Crossing between C and H had greater sca than other combinations at all ages studied, whereas B × Y had the smallest. Mean body weight of the offspring from two-line reciprocal cross differed according to their dam. A relatively large proportion of additive genetic effects in contributing to the variation in offspring body weight was indicated.

Key words: body weight, Diallel cross, mice

Introduction

The name "diallel" was introduced to denote all possible crosses among a number of parental types. Diallel cross can be divided into complete and the partial diallel crosses [5, 7]. The diallel cross experiment is useful for estimating the performance of breeds, strains or lines in hybrid combination in which the estimation is usually in terms of general combining ability (gca) and specific combining ability (sca). From the diallel cross, the other genetic effects such as heterosis, maternal ability and reciprocal effects of those breeds crossed can also be estimated.

The gca and sca concepts were first defined by Sprague and Tatum [21] in relation to corn breeding. The term gca is used to designate the average performance of a line in hybrid combinations. Estimation of gca may be used to rank lines for their potential as parents in a breeding program. The term sca is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the parental

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breeds, strains or lines involved.

Our previous study indicated that maternal effects were important in determining offspring body weight in mice [11]. The role of maternal effects has also been evaluated in detail in a cross-fostering experiment [12] in which the prenatal maternal effects were more important than postnatal maternal effects in contributing to the variation in offspring body weight. Offspring born to a large prenatal dam will be heavier than those born to a small dam whether nursed by a large or by a small postnatal dam.

Complete diallel cross experiments have been conducted on laboratory rat [8], mouse [15] and hamster [17], but until now no information has been reported on diallel cross using strains of mice with genetically distinctive and/or involving a small wild mouse.

For the above mentioned reason, complete diallel cross of the four genetic groups of mice which differ in body weight and genetical relationship was conducted. The objective of this study was to estimate the effects of sex, heterosis, general and specific combining abilities, maternal ability, and reciprocal cross on body weight at 1, 3, 6 and 10 weeks of age from all possible crosses among the mice.

Materials and Methods

Materials: The three genetic groups of laboratory mice (CF#1, C57BL/6NCrj and C3H/HeNCrj) and a genetic group of Yonakuni wild mice (*Mus musculus molossinus yonakuni*) were used as parental types. The laboratory mice had been maintained within a closed colony. The wild mice were trapped in the Ryukyu Islands (southern islands of Japan) in 1991 and have been mated within a closed colony since that time. The four genetic groups were subsequently designated C, B, H and Y. C and Y are the two lines which quite differ in body weight and litter size. C has large body, males weighing about 41 g and females about 34 g at maturity, and is apparently prolific with a litter size of about 12 mice. The body weight of Y is about 12–13 g at maturity and a mean litter size of 4 mice is recorded [19, 20]. Meanwhile, the other two genetic groups, B and H, were chosen because they are quite distinct from each other on the basis of polymorphic loci and a principal component analysis [22].

The four genetic groups were used to represent a complete 4×4 diallel cross design. From this design, four parental types, six F_1 crosses and six reciprocal F_1's were produced. A totals of 828 mice were used in this study.

The animal handling has been described in detail by Kurnianto *et al.* [10]. Basically, one male was mated with two to three females randomly when they reached nine to ten weeks of age, and they remained together for 16–21 days. The pregnant dams were taken and placed in separate cages until littering. Only the first litters were used. Litters were standardized to six young at birth; three males and three females where possible. Litters were weaned at three weeks of age. At weaning, litters were separated and caged based on sex. The trait measured in individuals was body weight from birth to ten weeks of age. Food pellets and water were provided *ad libitum.*

Statistical Analysis: Data analyzed in this study was body weight at 1 (Wk1), 3 (Wk3), 6 (Wk6) and 10 (Wk10) weeks of age. The least squares analysis used was basically formulated by Harvey [6] and modified by Satoh [18], and performed on all body weight data at each age studied.

The mathematical model is as follows:

$$Y_{ijklm} = \mu + s_i + h_j + p_{lk} + g_{2k} + g_{2l} + m_{2l} + c_{2kl} + r_{2kl} + e_{ijklm}$$

where

Y_{ijklm} = the m^{th} mouse of the i^{th} sex produced from a mating the k^{th} line of sire and the l^{th} line of dam in the j^{th} type of breeding (linebred, j=1 and linecross, j=2),
μ = the overall mean,
s_i = the effect of the i^{th} sex,
h_j = the effect of the j^{th} type of breeding,
p_{lk} = the effect of the linebred of the k^{th} line,
g_{2k} = the gca effect of the k^{th} line of sire,
g_{2l} = the gca effect of the l^{th} line of dam,
m_{2l} = the maternal effect of the l^{th} line of dam,
c_{2kl} = the sca effect of the k^{th} and l^{th} lines,
r_{2kl} = the reciprocal effect of the *kl* and *lk* crosses,
e_{ijklm} = the random error effect.

Heterosis for each cross was estimated separately by comparing the average performance of the linecross to the average performance of the linebred as presented by Kurnianto *et al.* [11]. The relative importance of gca and sca was studied by calculating the ratio of sum of squares, SSgca/(SSgca + SSsca), in which it is essentially the same as that proposed by Baker [1].

Results

The analysis of variance with mean squares for Wk1, Wk3, Wk6 and Wk10 is shown in Table 1. It is evident that all effects in the model constituted a highly significant source of variation (P<0.01) in body weight, except sex at Wk1 (P>0.05).

Computing least squares means is important in evaluating each effect contributing to the variation in body weight separately. Table 2 shows the least squares means of body weight for sex, heterosis and linebred. Sex difference was obtained from the pooled data of the four genetic groups. It can be seen that males were 0.40 g, 4.58 g and 5.62 g heavier than females (P<0.01) at Wk3, Wk6 and Wk10, respectively.

Highly significant difference (P<0.01) was observed between linebred and linecross for all ages (Table 1). The linecross exceeded the linebred by about 0.31 g, 1.03 g, 1.76 g and 1.40 g at Wk1, Wk3, Wk6 and Wk10, respectively (Table 2), and this amounted to 6.57%, 10.22%, 8.70% and 5.89% heterosis at the respective ages. In this study the heterosis was also estimated for each cross separately, expressed in weight units (g) and in percentages, shown in Table 3. CH,

Table 1. Analysis of variance of body weight and ratio of the general combining ability to total combining ability sum squares at 1 (Wk1), 3 (Wk3), 6 (Wk6) and 10 (Wk10) weeks of age

Source of variation	D.F.	Means Squares			
		Wk1	Wk3	Wk6	Wk10
Sex	1	1.896	33.157**	4322.117**	6527.650**
Heterosis	1	15.720**	180.710**	585.944**	330.296**
Linebred	3	203.843**	1571.483**	7312.009**	9923.343**
General combining ability	3	7.665**	58.357**	818.473**	1509.310**
Maternal effects	3	51.238**	195.582**	157.035**	169.311**
Specific combining ability	2	9.862**	7.131**	59.443**	20.059**
Reciprocal effects	3	3.937**	5.475**	11.413**	3.089**
Error	811	0.543	1.750	4.903	5.237
SSgca/(SSgca+SSsca)#		0.54	0.93	0.95	0.99

**Significant at p<0.01. #SSgca and SSsca: Sum of squares of general combining ability and specific combining ability, respectively.

Table 2. Least squares means of body weight at Wk1, Wk3, Wk6 and Wk10 for sex, heterosis and linebred

Classification	No.	Wk1	Wk3	Wk6	Wk10
Overall mean ($\hat{\mu}$)	828	4.87	10.60	21.17	24.45
Sex ($\hat{\mu} + \hat{s}_i$)					
Male	413	4.92[a]	10.80[a]	23.46[a]	27.26[a]
Female	415	4.82[a]	10.40[b]	18.88[b]	21.64[b]
Heterosis ($\hat{\mu} + \hat{h}_j$)					
Linebred	288	4.72[a]	10.08[a]	20.24[a]	23.76[a]
Linecross	540	5.03[b]	11.11[b]	22.00[b]	25.16[b]
Linebred ($\hat{\mu} + \hat{h}_l + \hat{p}_{lk}$)					
CC#	90	6.80[a]	16.26[a]	32.50[a]	37.80[a]
BB	48	4.68[b]	8.76[b]	17.94[c]	21.40[c]
HH	60	4.18[c]	8.77[b]	19.83[b]	23.51[b]
YY	90	3.20[d]	6.55[c]	10.70[d]	12.31[d]

#C, B, H and Y stand for CF#1, C57BL/6NCrj, C3H/HeNCrj and Yonakuni wild mouse, respectively. [a-d] Values with different superscript in the same column for each heading are significantly different at p<0.01.

Table 3. Heterosis effects on body weight at Wk1, Wk3,Wk 6 and Wk10 exhibited by each cross separately

Type of	No.	Wk1		Wk3		Wk6		Wk10	
Cross#		Unit (g)	%	Unit (g)	%	Unit (g)	%	Unit (g)	%
CB	96	−0.25	−4.36**	−0.05	−0.40	0.31	1.23	−0.52	−1.76*
CH	92	0.37	6.74**	0.60	4.75**	1.19	4.53**	1.26	4.09**
CY	150	0.10	2.00	0.27	2.32*	−0.42	−1.94*	−0.80	−3.17**
BH	72	0.70	15.80**	1.71	19.45**	2.86	15.12**	2.99	13.29**
BY	54	0.71	18.02**	1.91	24.89**	3.09	21.58**	2.05	12.16**
HY	76	0.28	7.59**	1.71	22.32**	3.48	22.76**	3.47	19.38**

* and **: Significant at $p<0.05$ and at $P<0.01$, respectively. #: For abbreviations, see Table 2.

BH, BY and HY crosses showed highly significant ($P<0.01$) positive heterosis at all ages studied. Negative heterosis was observed for CB at Wk1, Wk3 and Wk10, and for CY at Wk6 and Wk10. On average, heterosis effects tended to be small after weaning.

Differences among linebred performances of the pooled sexes were found at all ages studied (Table 2). Among the four genetic groups, C ranked highest in body weight at all ages: 6.80 g, 16.26 g, 32.50 g and 37.80 g at Wk1, Wk3, Wk6 and Wk10, respectively, whereas Y was the smallest, subsequently 3.20 g, 6.55 g, 10.70 g and 12.31 g at Wk1, Wk3, Wk6 and Wk10, respectively.

Table 4 shows the least squares means of body weight for gca, maternal effect, sca and reciprocal cross. C was superior to the other three genetic groups in gca at all ages studied, whereas Y was the smallest. Least squares means of body weight for C were 5.58 g, 13.29 g, 28.46 g and 33.98 g for Wk1, Wk3, Wk6 and Wk10, respectively. Moreover, the degree of superiority of gca can be ranked as C>H>B>Y.

Maternal effects measure the influence of the prenatal and postnatal maternal environments of a line. It can be seen in Table 4 that the maternal effects of C were superior to the other three genetic groups, and Y was the smallest. The maternal effects of H and B ranked between C and Y. The least squares means of body weight for C were 5.59 g, 12.84 g, 23.51 g and 26.11 g for Wk1, Wk3, Wk6 and Wk10, respectively; and for Y 4.15 g, 9.45 g, 20.57 g and 23.06 g.

Among the cross combinations (Table 4), crossing between C and H (CH) resulted in the heaviest body weight at all ages which indicated the highest sca effects for these traits. Crossing between B and Y resulted in the smallest body weight.

The ratios involving the SSgca/(SSgca + SSsca) are shown in Table 1. The closer the ratio is to unity, the greater the predictability is on the basis of gca alone for predicting cross performance. A ratio close to unity indicates much greater importance of additive gene effects than non-additive gene effects. The present study showed that the ratio was higher with increasing age, from 0.54 to 0.99.

Reciprocal cross analysis showed that the performance of the offspring depended on the line of the dam (Table 4). For example, when C was mated as the line of dam, offspring body weight was much heavier than when C was mated as the line of sire. The greater body weight of the offspring was obtained from the reciprocal cross between C and H (both CH and HC).

Discussion

The results of crossbreeding experiment with laboratory animals have provided a valuable interpretation of genetic analysis. Diallel cross analysis of this study has provided some estimates of the genetic effects on body weight simultaneously from the four genetic groups of mice used. In this study, a 4 × 4 diallel cross was conducted with three laboratory mice strains and a wild mouse strain that had been maintained within a closed colony.

Males surpassed females in body weight at weaning and thereafter. This agrees with findings reported by Nagai [15] who found that males were larger ($P<0.01$) at 25 and 45 days. Bakker *et al.* [2] also reported that males were significantly larger than females at Wk3, Wk6 and gain from 3 to 6 weeks, although the differ-

Table 4. Least squares means of body weight at Wk1, Wk3, Wk6 and Wk 10 for general combining ability, maternal effects and specific combining ability and reciprocal crosses

Classification	No.	Wk1	Wk3	Wk6	Wk10
General combining ability $(\hat{\mu} + \hat{h}_2 + 2\hat{g}_{2k})$					
C	338	5.58^{a}	13.29^{a}	28.46^{a}	33.98^{a}
B	222	5.33^{a}	10.50^{b}	21.54^{c}	23.08^{c}
H	240	4.71^{b}	10.59^{b}	23.09^{b}	27.26^{b}
Y	280	4.46^{b}	10.08^{c}	15.30^{d}	16.27^{d}
Maternal effects $(\hat{\mu} + \hat{h}_2 + \hat{m}_{2l})$					
C	192	5.59^{a}	12.84^{a}	23.51^{a}	26.11^{a}
B	126	4.84^{c}	10.92^{b}	21.67^{c}	25.49^{b}
H	109	5.24^{b}	11.25^{b}	22.63^{b}	25.93^{a}
Y	113	4.15^{d}	9.45^{c}	20.57^{d}	23.06^{c}
Specific combining ability $(\hat{\mu} + \hat{h}_2 + \hat{g}_{2k} + \hat{g}_{2l} + \hat{c}_{2kl} + (\hat{m}_{2k} + \hat{m}_{2l})/2)$					
CB	96	5.49^{b}	12.46^{b}	25.53^{b}	29.08^{b}
CH	92	5.86^{a}	13.11^{a}	27.35^{a}	31.93^{a}
CY	150	5.10^{bc}	11.68^{b}	21.18^{c}	24.26^{c}
BH	72	5.13^{bc}	10.47^{c}	21.74^{c}	25.44^{c}
BY	54	4.65^{d}	9.56^{cd}	17.41^{e}	18.91^{e}
HY	76	3.98^{e}	9.37^{d}	18.74^{de}	21.38^{d}
Reciprocal cross $(\hat{\mu} + \hat{h}_2 + \hat{g}_{2k} + \hat{g}_{2l} + \hat{c}_{2kl} + \hat{r}_{2kl} + \hat{m}_{2l})$					
CB#	48	4.98^{bc}	11.55^{c}	24.96^{b}	28.77^{b}
CH	38	5.76^{a}	12.38^{b}	26.93^{ab}	31.87^{a}
CY	60	4.04^{ef}	9.87^{e}	19.34^{fg}	22.72^{ef}
BH	24	5.33^{b}	10.89^{cd}	22.40^{cd}	25.88^{c}
BY	24	4.32^{de}	8.62^{f}	17.03^{g}	17.47^{h}
BC	48	6.01^{a}	13.37^{a}	26.09^{ab}	29.39^{b}
HY	29	3.63^{f}	8.80^{f}	17.90^{g}	20.17^{gh}
HC	54	5.96^{a}	13.83^{a}	27.77^{a}	31.98^{a}
HB	48	4.93^{bc}	10.06^{e}	21.08^{de}	25.00^{cd}
YC	90	6.15^{a}	13.48^{a}	23.02^{c}	25.79^{c}
YB	30	4.98^{bc}	10.50^{de}	17.79^{fg}	20.34^{fg}
YH	47	4.32^{de}	9.94^{e}	19.57^{efg}	22.58^{ef}

[a-h] Values with different superscripts in the same column for each heading are significantly different at $p<0.01$. # Sire × dam.

ence was small for Wk3.

Heterosis is an important phenomenon in animal breeding. Heterosis is said to occur when the average value in the linecross is higher for a particular trait than the linebred. Technically, heterosis effects can be either positive or negative [13]. In this study, on the basis of the results of the comparison of pooled linecross with the linebred, there were positive heterosis effects on body weight at all ages studied (Table 2), but the degree of heterosis effects would be large or small depending on the two-line cross combinations (Table 3). Negative values for heterosis occurred for the CB cross combination at Wk1, Wk3 and Wk10, and for CY at Wk6 and Wk10. These results were obtained because the average body weight of linecross was less than that of the linebred from which the linebred involved were mated. In addition, the negative heterosis in this study is possible due to the maternal effect, differences in body weight and the genetic distance between the parents. This study also indicated that crossing between genetically diverse lines exhibit of heterosis variation. Kurnianto *et al.* [11], who used CF#1 laboratory mouse and Yonakuni wild mouse, reported that heterosis effects in males were positively observed at Wk1, Wk3, Wk6 and Wk10, and were not significant. In females, however, negative heterosis effects were observed after weaning.

Maternal effects would occur in certain cross combinations. Differences in maternal ability are primarily attributable to differences in milk yield [9]. According to the analysis, the maternal effects of C were the highest in the four genetic groups and Y was the lowest. The maternal advantages in body weight given by C to the offspring might be consistent with a higher milk yield. Our unpublished data suggested that C had the highest milk yield (24.7 g), followed by H (20.2 g), B (15.3 g) and Y (7.4 g). The higher productivity in the milk yield may be related to anatomical development, assuming that the larger mice have larger mammary glands, and the anatomical component should be increased. This assumption seems to be true, because in fact C has a greater body weight than the other three genetic groups. Computations of average body weight at 10 weeks of age for C, H, B and Y females were 34.2 g, 19.6 g, 21.7 g and 12.1 g, respectively. Maternal effects refer to differences in offspring body weight caused by differences in the maternal environment provided by the dam during gestation and nursing. Legates [14] concluded that maternal effects play an important role in the early growth of laboratory mammals.

Gordon [4] stated that the additive genetic effects of each the parent involved in the cross, called gca, have two estimable qualities: 1) there is the gca value itself, usually expressed in units of the quantitative genetic character it represents, and 2) there is relative positioning or ranking of parental gca's as compared to each other. Of the two, the latter is clearly more important to the breeder. The differences in gca among the four genetic groups in the present study were highly significant at all ages (Table 1). Significant differences indicate the existence of additive gene action. The gca of C was the highest and was much different from the other three genetic groups at Wk3, Wk6 and Wk10. This suggested that the C might be an excellent parent in the cross.

Sca is a specific effect caused by interaction between the two parental genotypes, and reflects non-additive genetic action. It is assumed that sca contains the dominance and epistatic effects. As already shown in Table 1, there were significant effects of sca on variation in body weight at all ages. These results were in contrast to those observed by Nagai [15]: no significant effects of sca on average weight at birth, 12 and 25 days, but significant at 45 days. These may be due to the strains of mice used in calculating body weight. He used four inbred strains of laboratory mice, C3H/He, CBA/J, C57BL/6J and SWR/J, and the body weight analyzed was the average weight of individuals within a group. Meanwhile, this study involved the four genetic groups of mice, including small wild mice. As noted earlier, sca effects refer to the average inferiority or superiority of a cross relative to the average performance of the lines involved in that cross. It can be seen in Table 4 that sca tended to be large in cross combinations of laboratory mice, as exemplified by CB and CH crosses.

The ratio of the sum of squares of combining ability, SSgca/(SSgca + SSsca), informed the relative importance of gca and sca effects. The results of the present study showed stronger effects of gca on the variation in body weight as compared to sca at all ages. The ratios were more than 0.90 at Wk3, Wk6 and Wk10 (Table 1). This indicated that the preponderance of additive gene effects was higher than non-additive gene effects. This agrees with those of the statements pointed out by Sprague and Tatum [21], Kidwell and Howard [9] and Baker [1]. Roberts [16] reviewed the experimental results and concluded that non-additive effects contribute very little to variation in body weight in mice. Eisen *et al.* [3], who conducted an experiment to assess the type of genetic variability among the crosses of a random set of four light types and four heavy types in poultry, concluded that gca variance was the most important type of genetic variability for the majority of the traits studied. Sca variance was low in magnitude for most traits, indicating that dominance and epistatic variance was of little important.

Means body weight of the offspring from a two-line reciprocal cross in linebred strains should be similar because they receive the same autosomal-chromosomal contributions from either male or female parents. In fact in this study, the mean body weight of the offspring differed according to their dam. For example, the mean body weight of YC was greater than that of CY. The C dam possibly had a higher frequency of desirable allele that provided a maternal genotype superior that of the Y dam. Similar results were observed with other reciprocal cross combinations. These results indicated that the dam plays an important role in her effects on difference in offspring body weight. As pointed out by Williams *et al.* [23], the cytoplasmic differences peculiar to egg and sex-linked effects, as well as sampling of dams, are sources of reciprocal differences.

In conclusion, effects of heterosis, linebred, gca, sca, maternal ability and reciprocal cross constituted a highly significant source of variation in body weight at WK1, Wk3, Wk6 and Wk10. C had the greatest gca and maternal effects, whereas Y had the smallest. The additive gene effects were more important in contributing to the variation in offspring body weight than the non-additive gene effects.

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