Heterosis Effects of Body Weight and Jumping Height in Rotational Crossing of Two-Subspecies of Mice

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ABSTRACT : The present study was conducted to evaluate heterosis effects of body weight and jumping height for successive generations of rotational crossing using two subspecies of mice which are very different in body weight and in genetic relationship from each other. Domesticated laboratory mouse $CF_{\#1}$ (C) and Yonakuni wild mouse (Y) were used as materials. Two groups of rotational crossing was made according to the parent used at the beginning of crosses, C male×Y female and Y male×C female. These crosses were done to produce the first (G_1 and G_1'), second (G_2 and G_2') and third generations (G_3 and G_3') with sire used was alternated. Individual body weights were weighed at 1 (wk1), 3 (wk3), 6 (wk6) and 10 weeks of age (wk10) and jumping heights were measured at six weeks of age (wk6). Only the first litter used. For body weight, results of this study showed that genetic group effects were significant (p<0.01) source of variation at all ages studied. Sex effects were significant (p<0.01) at wk3, wk6 and wk10, but not at wk1. Significant interaction effects (p<0.01) between genetic group and sex were found at wk6 and wk10. The C mice with large maternal effects produced heavier offspring body weight and crosses using sire of this subspecies maintained heavy weight compared to wild Y mouse sire that has small body size. Heterosis tended to exist at the rotational crossing started from Y male C female. For jumping height, effects of genetic group and sex were significant, sire and dam effects (heterosis) exhibited from the first to third generations, and no maternal effects were observed. *(Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 7 : 888-893)*

Key Words : Rotational Crossing, Two-Subspecies of Mice, Body Weight, Jumping Height, Heterosis

INTRODUCTION

Crossbreeding is an effective mating system for increasing animal production by combining the desirable characteristics of two or more breeds and by increasing the levels of performance for particular traits due to heterosis. Long (1980) stated that decision regarding crossbreeding involve choice of breed and design of combination or crossing scheme.

Perhaps the simplest long range crossbreeding is two-breed rotation. In this system, the replacement females are bred to males of the opposite breed in succeeding generations. Systematic rotational crossing permits production and selection of replacement females as well as one that includes the beneficial effects of heterosis (Dickerson, 1969).

Previous evaluations of rotational crossing with cattle have been reported for calf performance to weaning (Crocket et al., 1978; Neville et al., 1984). They concluded that two- and three-breed rotational crossing systems are effective and practical procedures for maintaining the advantage of heterosis.

There is a paucity of information about the effects of rotational crossing on body weight and jumping height in different subspecies of mice. Experimental results to verify heterosis effects from this crossing are also lacking.

This study was designed to evaluate heterosis effects of body weight and jumping height during successive generations of rotational crossing using two subspecies of mice, i.e. wild and laboratory mice, which are very different in body weight and in genetic relationship from each other.

MATERIALS AND METHODS

Mice

Two subspecies of mice, the $CF_{\#1}$ laboratory mouse (C, *Mus musculus domesticus*) and Yonakuni wild mouse (Y, *Mus musculus molossinus yonakuni*) were used as the basic materials. The description and breeding history of these two subspecies have been described by Kurnianto et al. (1997) and Kurnianto et al. (1998a).

In this study, sire was written precedes dam. Reciprocal rotational crossing was made according to the parent used at the beginning of crosses, that was C×Y and Y×C. Crosses between these two subspecies to produce reciprocal first generation (G_1 and G_1'), 1/4～3/4 backcrosses from the first generation (G_2 and G_2') and 3/8～5/8 crosses (G_3 and G_3') were made by mating one male and two to three females when they reached nine to ten weeks of age. Mating design, gene proportion and number of mice used are presented in table 1.

At birth, litters were standardized to six mice, three males and three females as near as possible. The

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Table 1. Mating design, gene proporation and number of mice

Mating group	Genetic group (Sire × Dam)[1]	Generation	Gene proportion[2]		Number of mice	
			C	Y	Male	Female
Parental types						
	C×C	0	100	0	45	45
	Y×Y	0	0	100	46	44
Reciprocal rotational crossing						
	C×Y	1	50	50	31	37
	Y×CY	2	25	75	23	23
	C×YCY	3	62.5	37.5	25	23
	Y×C	1'	50	50	45	45
	C×YC	2'	75	25	21	26
	Y×CYC	3'	37.5	62.5	30	35

[1] C : Domesticated laboratory mouse $CF_{\#1}$, Y : Yonakuni wild mouse.
[2] Percentage of the gene proportion for C and Y at each generation.

Table 2. Analysis of variance for body weight at wk1, wk3, wk6 and wk10

Source of variation	D.F.	Means squares			
		wk1	wk3	wk6	wk10
Genetic group	7	128.68**	768.19**	3,449.36**	4716.36**
Sex	1	1.41	32.90**	3,436.45**	4977.30**
Genetic group×sex	7	0.33	0.94	117.21**	167.27**
Error	528	0.55	2.07	4.17	5.98

** Significant at p<0.01.

standardization of litter size was important to eliminate the effects of the number of litter suckled. Mice were weaned at three weeks of age. At weaning, males and females were caged separately with three mice per cage. Water in drinking bottle and food pellets (CE-2, Clea Japan Inc.) were provided *ad libitum*. Room temperature was maintained at approximately 24℃ and 70% relative humidity.

Only first litters were used. Individual body weights were weighed from birth to ten weeks of age with Sartorius portable (model PT-1200, 0.1 g scale) and individual jumping heights were measured at six weeks of age by using shock tool during 15 second. Tool set and procedure for measuring jumping height has been described in detail by Kurnianto et al. (1999).

Statistical analysis

Data used in this study were individuals body weight at 1 (wk1), 3 (wk3), 6 (wk6) and 10 (wk10) weeks of ages, and jumping height at wk6. Our previous study showed that there were no significant differences in the first, second and third jumping heights (Kurnianto et al., 1999). According to this result, in the present study individuals measurement were restricted to the first three jumping heights, and average jumping height was calculated from these data. Both body weight and jumping height data were analyzed using GLM of SAS (1990) with following mathematical model:

$$Y_{ijk}=\mu+G_i+S_j+(GS)_{ij}+e_{ijk}$$

where Y_{ijk}=an observation on the k^{th} mouse of the j^{th} sex in the i^{th} genetic group; μ=overall mean; G_i=effects of the i^{th} genetic group (i=1, ..., 8); S_j=effects of the j^{th} sex (j=1, 2); $(GS)_{ij}$=interaction effects between genetic group and sex; and e_{ijk}=random error.

Duncan's multiple rage test was used to examine means comparison of genetic group-sex subclass. Linear contrasts were performed to compare mid-parent to crossbred at successive generations for each sex in estimating heterosis effects on the basis of Kurnianto et al. (1998b).

RESULTS

Body weight

Mean squares for body weight at wk1, wk3, wk6 and wk10 from analysis of variance are presented in table 2. Genetic group was significant (p<0.01) source of variation for body weight at all ages studied, suggesting that litters body weight among genetic groups were different depending on the mating type of the parent. Sex effects significantly ($p<0.01$) affected body weights at wk3, wk6 and wk10, but not for those at wk1. Interaction effects of genetic group and sex were found after weaning, that was wk6 and wk10.

We observed that mean body weight at wk10, age considered for mating mice, for C was 41.17 and 31.57 g for males and females, respectively, whereas for Y was 14.16 g for males and 12.25 for females (Kurnianto et al., 1998b). Reciprocal rotational crossing between these two subspecies of mice in the present study resulted in the opposite patterns of mean body weight at successive generations. Figures 1 and 2 present the patterns of mean body weight at wk3 and wk10 from the first to third generations at the two rotational crossing group for males and females, respectively. The C×Y mice (G_1) were significant ($p<0.01$) lighter body weight than Y×C (G_1'). For example at wk10, C×Y mice had 25.90 and 19.39 g for males and females, respectively, whereas Y×C was 30.37 and 21.74 g. This indicated that there was a larger maternal effect at C dams. Furthermore, this study also showed that crossing with use of large mice sire (subspecies C) tended to increase body weight as shown by C×YC (G_2') for both sexes. Body weight, then, decreased in Y×CYC (G_3') after they were mated with small size Y sire. In contrast to these results, mice at the G_2 from Y sire (Y×CY) revealed lighter body weight, and the body weight of offspring increased again as C sire used at the G_3 (C×YCY). These findings suggested that sire apparently has also a role in contributing to the performance of body weight.

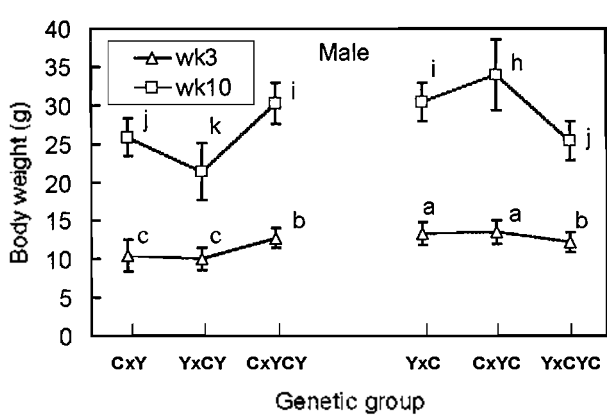

Figure 1. Mean body weight at male mice of two groups of rotational crossing at wk3 and wk10. Vertical lines represents standard deviation. Different letters at each age indicate significant difference at $p<0.05$.

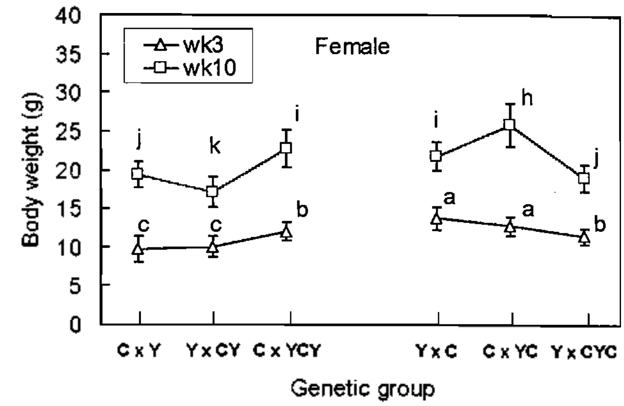

Figure 2. Mean body weight at female mice of two groups of rotational crossing at wk3 and wk10. Vertical lines represents standard deviation. Different letters at each age indicate significant difference at $p<0.05$.

Jumping height

Analysis of variance with mean square for jumping height at wk6 is presented in table 3. It can be seen, genetic group and sex significantly contributed to the variation of jumping height ($p<0.05 \sim p<0.01$). No interaction between genetic group and sex found in this study.

Table 3. Analysis of variance for jumping height at wk6

Source of variation	D.F.	Mean square
Genetic group	6	55.76*
Sex	1	71.73**
Genetic group×sex	6	6.62
Error	245	9.16

* Significant at $p<0.05$; ** Significant at $p<0.01$.

The average jumping height for both sexes are presented in table 4. All C mice did not show jumping activity, while other genetic groups showed jump with different percentage ranged from 30.0~77.4% for males and 21.7~73.9% for females that were calculated from total mice observed at each genetic group. Y×Y attained the lightest average jumping height about 17.9 and 16.5 cm for males and females, respectively; C×Y attained the highest, about 20.9 cm for males and 20.1 cm for females. Meanwhile, there were similarity in average jumping height for other five genetic groups of rotational crossing, ranged from 18.8~20.3 cm for males and from 17.7~18.8 cm for females. No maternal effects found for jumping height in this study.

Heterosis effects

Tables 5 and 6 present heterosis effects for body

Table 4. Average jumping height at male and female from reciprocal rotational crossing of two subspecies of mice

Mating group	Genetic group	Generation	Male N[1]	Male J[2]	Male Average[4]	Female N	Female J	Female Average
Parental types								
	C×C	0	45	0 (00.0)[3]	0.0	45	0 (00.0)	0.0
	Y×Y	0	44	34 (77.2)	17.9±2.0[b]	46	34 (73.9)	16.5±3.1[b]
Reciprocal rotational crossing								
	C×Y	1	31	24 (77.4)	20.9±3.4[a]	37	27 (72.9)	20.1±3.4[a]
	Y×CY	2	23	14 (60.8)	18.8±2.1[ab]	23	18 (73.2)	18.4±3.8[ab]
	C×YCY	3	25	8 (32.0)	19.3±3.9[ab]	23	5 (21.7)	17.7±1.9[ab]
	Y×C	1'	45	24 (53.3)	18.8±3.0[ab]	45	31 (68.9)	18.8±3.2[ab]
	C×YC	2'	21	8 (38.1)	20.2±2.4[ab]	26	9 (34.6)	18.1±2.4[ab]
	Y×CYC	3'	30	9 (30.0)	20.3±3.0[ab]	35	13 (37.1)	17.7±2.9[ab]

[a,b] Means among genetic groups without common superscripts within sex are significantly different at $p<0.05$.
[1] The number of mice used. [2] The number of mice showed jumping activity.
[3] Numbers in the parenthesis represent percentage of mice jumped (J/N×100).
[4] Average jumping height calculated from the first, second and third jumping heights.

Table 5. Heterosis effects for body weight at wk1, wk3, wk6 and wk10

Genetic group	Generation	wk1 Unit	wk1 %	wk3 Unit	wk3 %	wk6 Unit	wk6 %	wk10 Unit	wk10 %
Male									
C×Y	1	-0.37**	-7.91	-0.42**	-3.82	-1.37**	-5.82	-1.57**	-5.72
Y×CY	2	0.13*	2.71	-0.81**	-7.41	-4.50**	-19.11	-6.10**	-22.21
C×YCY	3	0.45**	9.64	1.89**	17.35	3.31**	14.06	2.81**	10.23
Y×C	1'	1.44**	31.09	2.44**	22.41	2.25**	9.55	2.90**	10.56
C×YC	2'	1.34**	28.93	2.65**	24.34	6.12**	25.99	6.48**	23.59
Y×CYC	3'	0.78	16.79	1.33**	12.20	-0.23*	-0.98	-2.08**	-7.57
Female									
C×Y	1	-0.57**	-12.58	-0.86**	-8.14	-2.37**	-12.36	-2.79**	-12.58
Y×CY	2	0.31**	6.62	-0.55**	-5.20	-3.80**	-19.81	-5.05**	-22.77
C×YCY	3	0.72**	15.89	1.40**	13.25	1.63**	8.50	0.61*	2.75
Y×C	1'	1.43**	31.57	3.15**	29.80	0.89**	4.64	-0.44*	-1.98
C×YC	2'	1.18**	26.05	3.14**	29.71	3.80**	19.81	3.64**	16.41
Y×CYC	3'	0.72**	15.89	0.89**	8.42	-1.50**	-7.82	-3.15**	-14.20

Heterosis unit, h=[average of rotational crossbred - average of initial parental types]; h%=(h/average of initial parental types)×100.
* Significant at $p<0.05$; ** Significant at $p<0.01$.

Table 6. Heterosis effects for jumping height at wk6

Genetic group	Generation	Heterosis at male Unit	Heterosis at male %	Heterosis at female Unit	Heterosis at female %
C×Y	1	11.95**	133.52	11.85**	143.64
Y×CY	2	9.85**	110.06	10.15**	123.03
C×YCY	3	10.35**	115.64	9.45**	114.55
Y×C	1'	9.85**	109.06	10.55**	127.88
C×YC	2'	11.25**	125.70	9.85**	119.39
Y×CYC	3'	11.35**	126.82	9.45**	114.35

** Significant at $p<0.01$.

weight and jumping height, respectively. C×Y crosses resulted in negative heterosis effects on body weight at all ages of G_1, -0.37~-5.72% for males and -0.57~-12.58% for females. This means that crossbred mice had lighter body weight compared to those of their mid-parents. Negative heterosis effects were still indicated in G_2 at wk3, wk6 and wk10, -0.81~-22.21% for males and -5.20~-22.77% for females. C sire increased body weight in G_3 and this caused positive heterosis. Results in rotational crossing started from Y×C were different from those from C×Y, in which the significant positive heterosis was attained in G_1 and G_2, while negative heterosis effects were in wk6 and wk10 of G_3. This is probably due to interaction effects of the parents mated.

Heterosis effects for jumping height were over 100% (109.06~143.64%) because of no jumping activity in C parents. Furthermore, average jumping height at crossbred from C×Y rotational crossing tended to decrease and this caused decreasing in heterosis.

DISCUSSION

In two-breed rotational crossing originated from reciprocal crossbred, the genotype of the progeny at the second generation has different proportions (3/4 or 1/4) of the original breeds represented, depending on the sire used (Pattie et al., 1990; Van Vleck et al., 1987). For all subsequent generations, the breed of the sire is alternated, giving the different proportions of the breed across generations. This system reaches equilibrium at 2/3 of genes from the most recent sire breed and 1/3 from the other breed. It takes four generations for the proportions to approach their stable level. A point of interest is that heterotis observed in each generation decreases. At equilibrium, however, about 66 percent of the potential heterosis response are maintained. Implications for farm animal are that it does not require large numbers, it does utilize hybrid dams and is an easily managed system. It is important to note how two breeds will complement each other or in other word is the combining of desirable traits from two different breeds into one unit. Strength in one breed will often take up for weakness in another breed.

In the present study, rotational crossing was conducted for three generations. Therefore, equilibrium in blood percentage (gene proportion) between two subspecies of mice used was not attained yet. The basic mating at the base group was different depending on the sire and dam used (C×Y and Y×C). The consequence was that blood percentage of subspecies C and Y were also different at each generation between these two groups. An example for the third generation, offspring from C×Y base group of rotational crossing would have 5/8 and 3/8 for blood percentage of subspecies C and Y, respectively. In contrast, Y×C base group gave respective 3/8 and 5/8 of blood percentage of subspecies C and Y to the offspring. Analysis between these two groups are necessary to compare which crossing types provide optimize production traits at short breeding time. Analysis of variance showed that both sire and dam, obviously, play an important role in contributing traits to the offspring. It was indicated that subspecies of sire and of dam and their interaction effects were highly significant source of variation. The C sired mice were heavier than the Y sired mice. Moreover, existence of heavier maternal effects of C dam increased their offspring weight. This suggested that a cross using large sire and (or) dam strongly suggested to improve performance of offspring weight. Of the all genetic groups, on the whole, C×YC attained the heaviest body weight after weaning.

Performance of parents also affected the offspring behavior such as jumping activity (Smith, 1972), which was observed almost exclusively in the wilds. In the present study, jumping activity is considered as a measure of the vigor for this behavioral trait, and expressed in jumping height. There were no differences in average jumping height between the first, second and third generations for both two groups of rotational crossing.

It seems reasonable that wild mice have been selected for tameness by the process of domestication, thus domesticated laboratory mice tended to have homozygous gene for tameness (Dawson, 1932). In the present study, domesticated laboratory mice C did not show jumping activity. Meanwhile Y wild mice showed vigorous with average jumping height about 17.9 cm for males and 16.5 cm for females. Although no maternal effects found, the similar activity at the first generation was maintained in the successive generations of the rotational crossing.

Heterosis is an important phenomenon in animal breeding (Pattie et al., 1990), it can be used for increasing efficiency in continuous crossing system or it can cause problems with the interpretation of experiments aimed at finding suitable combination of breeds. The amount of heterosis and the advantage to be gained by crossbreeding largely depend on the degree of genetic difference between the breeds used. The present study showed that gene proportions and maternal effects of the parents affected heterosis on offspring body weight. If gene proportion of Y was high in the cross (more than 50%), besides the smaller maternal effects of Y dams compared to C dams, then body weight of the offspring tended to be light and this resulted in the negative heterosis. Rotational crossbred progeny at the G_1 and G_2 exhibited the negative heterosis for body weight (see table 5). In relation to these results, as shown table 1, the gene proportion of Y at G_1 was originated only from Y dams. While the gene proportion of Y at G_2 consisted of 50% sires and 25% dams. Furthermore, the negative heterosis effects appeared at G_3, in which the gene proportion of Y consisted of 56.25% sires and 6.25% dams. Positive heterosis effects were attained when C gene proportion was higher.

It was found in this study that heterosis effects for jumping height were over 100%. As pointed out by Pattie et al. (1990), heterosis tends to have greatest effects on fitness characters. The diallel genetic analysis on behavioral traits conducted by Smith and Connor (1974) indicated few instances of dominance variation or heterosis. Jumping was one of those of not demonstrating significant additivity.

The findings of the present study suggest that it is considerable from subspecies of sire and of dam in contributing the variation of body weight at the successive generations. Domesticated large C mice with large maternal effects produced heavier offspring body weight and crosses using sire of this subspecies maintained heavy weight compared to wild Y mouse sire that has small body size. For jumping trait, large effects of sire and dam exhibited in the first generation and tended to maintain at successive generation.

REFERENCES

Crocket, J. R., M. Koger and D. E. Franke. 1978. Rotational crossbreeding of beef cattle: Preweaning traits by generation. J. Anim. Sci. 46:1170-1177.

Dawson, W. M. 1932. Inheritance of wildness and tameness in mice. Genetics. 17:296-326.

Dickerson, G. E. 1969. Experimental approachs in utilizing breed resources. Anim. Breed. Abstr. 37:191-202.

Kurnianto, E., A. Shinjo and D. Suga. 1997. Comparison of the three growth models for describing the growth the growth patterns in wild and laboratory mice. J. Vet. Epidemiol. 11:49-55.

Kurnianto, E., A. Shinjo and D. Suga. 1998a. Analysis of growth in intersubspecific crossing of mice using Gompertz model. Asian-Aus. J. Anim. Sci. 11:84-88.

Kurnianto, E., A. Shinjo and D. Suga. 1998b. Average direct and maternal genetic effects and heterosis effects on body weight in two subspecies of mice. Asian-Aus. J. Anim. Sci. 11:475-479.

Kurnianto, E., A. Shinjo and D. Suga. 1999. The inheritance of jumping activity in reciprocal cross of two subspecies of mice. Asian-Aus. J. Anim. Sci. 13:733-738.

Long, C. R. 1980. Crossbreeding for beef production: experimental results. J. Anim. Sci. 51:1197-1223.

Neville, Jr. W. E., B. G. Mulllinix, Jr. and W. C. McCormick. 1984. Grading and rotational crossbreeding of beef cattle. II. Calf performance to weaning. J. Anim. Sci. 58:38-46.

Pattie, W. A., H. Martojo, L. Iniquez and S. S. Mansjoer. 1990. Second Workshop in Animal Breeding on Use of Computer Programs in Animal Breeding. IPB-Australia Project, Bogor, Indonesia.

SAS. SAS/STAT User's Guide. Volume 2, Version 6, Fourth Edition. SAS Institute Inc., SAS Campus Drive, Cary. NC27513.

Smith, R. H. 1972. Wildness and domestication in *Mus musculus*: A. Behavioral analysis. Journal of Comparative and Physiological Psychology. 79:22-29.

Smith, R. H. and J. L. Connor. 1974. The inheritance of behavioral wildness in house mice (*Mus musculus L.*). Animal Learning and Behavior. 2:249-258.

Van Vleck, L. D., E. J. Pollak and E. A. B. Oltenacu. 1987. Genetics for the Animal Sciences. W. H. Freeman and Company, New York.