Heterosis Effects on Jumping Height and Body Weight in Three-Way Rotational Crossing in Mice

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ABSTRACT: The three-way rotational crossing experiment has been conducted to evaluate heterosis effects on jumping height and body weight. Yonakuni wild mice (Y) and two genetic groups of CF#1 (C) and C3H/HeNCrj (H) laboratory mice were used as materials. Reciprocal rotational crossing was made by crossing C male × Y female and Y male × C female to produce basic group designated G₀ and G₀', respectively. The females of the G₀ and G₀' were mated to the H sire to produce second generation (G₁ and G₁'), and at the following generation the replacement females were mated to Y or C sire according to the basic group to produce G₂ to G₃ and G₂' to G₃'. Individual jumping height data at Wk6 and body weight data at 1 (Wk1), 3 (Wk3), 6 (Wk6) and 10 (Wk10) weeks of age were analyzed. The results showed that effects of genetic group, sex and interaction of genetic group by sex were significant (p<0.01) for jumping height. For males, 55.3 4%~79.17% and 54.46%~78.29% of heterosis were reached at G₁ to G₃ and G₁' to G₃', respectively. While for females at G₁ to G₃ and at G₁' to G₃', heterosis effects were 61.53%~80.42% and 47.79%~85.86%, respectively. For body weight, genetic group was a significant source of variation at all ages studied. Sex effect was significant at Wk3, Wk6 and Wk10, and interaction between genetic group and sex was significant at Wk6 and Wk10 (p<0.01). C sires resulted in the highest body weight of offspring, while H sires were the intermediate and Y sires were the lightest. The significant positive and negative heterosis effects for body weight were exhibited. Crossing involved the Y sires in addition to smaller maternal effects of Y dams tended to result in small heterosis. (Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 10: 1353-1358)

Key Words: Jumping Height, Body Weight, Heterosis, Rotational Crossing, Mice

INTRODUCTION

Heterosis has been the subject of much research because of its important implication for breeding programs. The amount of heterosis and the advantage to be gained by crossbreeding largely depend on the degree of genetic difference between the breeds used. Heterosis effects are greatest among crosses between widely different breeds and heterosis tends to have greatest effects on fitness traits. Lasley (1978) pointed out that heterosis is caused by heterozygosity involving genes with non-additive effects. Non-additive genes include dominance, overdominance and epistasis.

It was pointed out by Neville et al. (1984) that a practical crossbreeding system should produce its own female replacements. One of the crossbreeding systems that permits production and selection of female replacements as well as one that includes the beneficial effects of heterosis is rotational crossing (Dickerson, 1969). In three-breed rotational crossing, the herd tend to stabilize in breed percentage of approximately 57%, 29% and 14% blood of each breed in the sequence of the most recently used breed of sire (Van Vleck et al., 1987). The three-breed

Kurnianto et al. (2000b) conducted an experiment of reciprocal two-subspecies rotational crossing by use of two distinct types of mice, CF_{#1} laboratory mice (C) and Yonakuni wild mice (Y) to evaluate heterosis effects on body weight and jumping height. It was concluded that heterosis effects for body weight existed in the first and second generations from parental crossing of Y male×C female. For jumping height, large effects of sire and dam were exhibited in the first generation and tended to be maintained in successive generations.

A further experiment on three-way rotational crossing effects on jumping height and body weight in mice is necessary; therefore, this study was designed to evaluate heterosis effects on those two traits during successive generations of rotational crossing using three strains of wild and laboratory mice which are different in body weight and genetic relationships.

MATERIALS AND METHODS

Mice

Three genetic groups of mice, namely Yonakuni wild mice (Y) and two strains of laboratory mice designated CF_{#1} (C) and C3H/HeNCrj (H), were used in this study and determined as parental types. The description, breeding history and management for these

rotational crossing maintains a higher degree of heterosis than two-breed system; theoretically, 86% of the potential heterotic response is maintained.

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animals have been described by Kurnianto et al. (1997) and Kurnianto et al. (1998a).

The basic groups (generation 0) were mice produced from reciprocal two-way crosses of $C\times Y$ and $Y\times C$ (sire precedes dam). The females of $C\times Y$ and $Y\times C$ were mated to sires of the third strain, H, to produce first generation G_1 ($H\times CY$) and G_1 ' ($H\times YC$). For the successive generations, the replacement females were mated to Y or C sires according to the basic group to produce G_2 ($Y\times HCY$) and G_3 ($C\times YHCY$), G_2 ' ($C\times HYC$) and G_3 ' ($Y\times CHYC$). The mating design, gene proportions and the number of mice in detail are presented in table 1.

At the first parity litter, individual body weights were weighed from birth to ten weeks of age. Meanwhile, individual jumping heights for the first three jumping were measured at six weeks of age using a shock tool during 15 seconds. Tool set and the procedure for measuring jumping height have been described by Kurnianto et al. (2000a).

Statistical analysis

Individual jumping height data at six weeks of age (Wk6) and body weight data at Wk1, Wk3, Wk6 and Wk10 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; e_{ijk} = random error

Duncan's multiple range test was performed to compare performances among genetic group-sex subclass. Linear contrasts were used 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

Jumping height

Table 2 shows analysis of variance for jumping height at Wk6. As shown, genetic group, sex and interaction effects between genetic group and sex were significant source variation (p<0.01). It was important, therefore, to conduct a further analysis for comparing the genetic group on jumping activity at each sex. Average jumping height at males and females from the reciprocal three-way rotational crossing are presented in table 3. As shown at the parental types, CXC of both sexes did not jump throughout the experiment. Y × Y showed 77% and 74% jumping for and females, respectively, and H×H demonstrated 50% for males and 46% for females. No differences in average jumping height were found between $Y \times Y$ and $H \times H$ either for males or females; jumping height ranged from 16.1 to 17.9 cm. For the successive generations, the number of mice that jumped was decreasing. There were no differences in average jumping height for the six genetic groups of rotational cross males (ranged from 17.5 to 20.3 cm). However, average jumping height was slightly more variable for females (ranged from 16.3 to 20.5 cm). Furthermore it can be seen in table 3, average jumping height at pooled parental type significantly lower compared with the offspring at pooled reciprocal rotational crossing.

Body weight

Analysis of variance with mean squares for body

Table 1. Mating design, gene proportion and the number of mice in three-way rotational crossing

Mating group	Genetic group	Generation	Gene proportion (%) ²			Number of mice	
	$(Sire \times Dam)^1$		С	Y	Н	Male	Female
Parental types							
	$C \times C$	0	100	0	0	45	45
	$\mathbf{Y} \times \mathbf{Y}$	0	0	100	0	44	46
	$H \times H$	0	0	0	100	42	46
Reciprocal rotation	nal crossing			•			
	$H \times CY$	1	25	25	50	22	20
	$Y \times HCY$	2	12.5	62.5	25	24	30
	$C \times YHCY$	3	56.25	31.25	12.5	16	21
	$H \times YC$	1'	25	25	50	21	23
	$C \times HYC$	2'	62.5	12.5	25	21	21
	$Y \times CHYC$	3'	31.25	56.25	12.5	20	22

¹ C: Domesticated laboratory mouse CF_{#1}; Y: Yonakuni wild mouse.

² Percentage of gene proportion for C, Y and H at each generation.

Table 2. Analysis of variance for jumping height at Wk6

Source of variation	D.F.	Mean square
Genetic group	7	30.64**
Sex	1	8.33**
Genetic group × sex	7	10.75**
Error	176	6.27

^{**} Significant at p<0.01.

weight at Wk1, Wk3, Wk6 and Wk10 are presented in table 4. Genetic group was a significant source of variation (p<0.01) that affected body weight at all ages examined. Sex effect was significant at Wk3, Wk6 and Wk10 (p<0.01), but not significant at Wk1 (p>0.05). Interaction between genetic group and sex was significant at Wk6 and Wk10 (p<0.01).

Mean body weights of reciprocal three-way

rotational crossing are illustrated in figures 1 and 2 for males and females, respectively. As shown in the figures, the performance of body weight in the successive generations was affected by the strain of sire. Decreasing body weights in G_2 offspring were observed after mating G_1 to Y sire and then they increased after using sire C (G_3) . The results for G_2 ' and G_3 ' were consistent with increasing and decreasing body weight subsequently after mating them to C and Y sire. On the whole, C sires resulted in the highest body weight of offspring, while H sires were the intermediate and Y sires were the lightest. It seemed that sire had a role in contributing to offspring body weight.

Heterosis effects

Table 5 shows heterosis effects for jumping height at Wk6. As shown, significant heterosis effects were

Table 3. Average jumping height at male and female from reciprocal rotational crossing of three strains of mice

Mating types	Genetic group	Generation	Male				Female		
		(G)	N ¹	J^2	Average ³	N	· J	Average	
Parental types (PT)									
	$C \times C$	0	45	$0(00.0)^4$	0.0	45	0(00.0)	0.0	
	$\mathbf{Y} \times \mathbf{Y}$	0	44	34(77.2)	17.9 ± 2.0^{ab}	46	34(73.9)	$16.5 \pm 3.1^{\circ}$	
	$H \times H$	0	42	21(50.0)	16.1 ± 1.1^{b}	46	21(45.7)	$16.6 \pm 2.2^{\circ}$	
	Pooled for PT		131	55(42.0)	11.3 ± 1.9^{q}	137	55(40.2)	11.0 ± 2.8^{q}	
Reciprocal rota	ational crossing								
	$H \times CY$	1	22	12(54.6)	17.6 ± 2.1^{ab}	20	8(40.0)	19.9 ± 1.9^{ab}	
	$Y \times HCY$	2	24	8(33.3)	19.5 ± 2.2^{ab}	30	7(23.3)	$18.1 \pm 2.4^{ m abc}$	
	$C \times YHCY$	3	16	1 (6.3)	20.3 ± 3.0^{a}	21	5(23.8)	$17.8\pm5.4^{\rm abc}$	
	Pooled I		62	21(33.9)	19.2 ± 3.2^{P}	71	20(28.2)	$19.2 \pm 3.4^{\rm p}$	
	$H \times YC$	1'	21	6(28.6)	20.2 ± 4.7^a	23	5(21.7)	20.5 ± 1.5^{a}	
	$C \times HYC$	2'	21	6(28.6)	17.5 ± 2.7^{ab}	21	8(38.1)	17.1 ± 2.7^{bc}	
	$Y \times CHYC$	3'	20	6(30.0)	18.4 ± 3.0^{ab}	22	7(31.8)	16.3 ± 2.1^{c}	
	Pooled II		62	18(29.0)	18.7 ± 3.1^{P}	66	20(30.3)	18.4 ± 3.0^{P}	

a,b Means among genetic groups within sex with different superscript are significantly different at p<0.05.

Table 4. Analysis of variance for body weight at Wk1, Wk3, Wk6 and Wk10 in three-way rotational crossing

•	•						
Source of variation	D.F.	Mean squares					
		Wk1	Wk3	Wk6	Wk10		
Genetic group	8	90.17**	664.05**	2931.62**	3969.29**		
Sex	1	0.94 ^{NS}	43.91**	2643.23**	3719.59**		
Genetic group × sex	8	0.31 ^{NS}	2.94 ^{NS}	104.48**	108.90**		
Error	513	0.57	2.31	3.80	5.01		

^{**} Significant at p<0.01.

p.q Means among pooled groups within sex with different superscript are significantly different at p<0.05.

¹ The number of mice used.

² The number of mice showing jumping activity.

³ Average jumping height calculated from the first, second and third jumping heights.

⁴ Numbers in the parentheses represent percentage of mice that jumped (J/N×100).

Non significant (p>0.05).

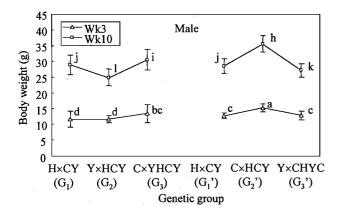


Figure 1. Mean body weight of male mice at rotational crossing at Wk3 and Wk10. Vertical lines represent standard deviation. Different letters among generations at each age indicate significant difference at p<0.05

attained from the first to the third generation. For males, $55.34\% \sim 79.17\%$ and $54.46\% \sim 78.29\%$ of heterosis were reached at G_1 to G_3 and G_1 ' to G_3 ', respectively; for females at G_1 to G_3 and at G_1 ' to G_3 ', heterosis effects were $61.53\% \sim 80.42\%$ and $47.79\% \sim 85.86\%$, respectively. Furthermore for pooled data from the three generations, heterosis effects in the population started from $C \times Y$ (pooled I) were higher than those in the population from $Y \times C$ (pooled II) for both sexes.

Table 6 shows heterosis effects for body weight at Wk1, Wk3, Wk6 and Wk10. Significant positive and negative heterosis effects for body weight were observed in this study. Negative heterosis existed in males at Wk6 and Wk10 of G_2 (-7.65% \sim -6.94%). In females, negative heterosis occurred at Wk6 and Wk10 of G_1 (-2.43% \sim -0.07%), G_2 (-11.76% \sim -10.28%) and G_3 ' (-8.30% \sim -7.45%).

DISCUSSION

The three-way rotational crossing is not different from the two-way rotational cross except it requires three strains and does not include a backcross, and heterozygosity stabilizes after seven generations. Because of wide fluctuation between generations in gene proportion in rotational crossing, the strain used should be reasonably comparable in traits, in which the traits considered in the present study were jumping height and body weight. Crossing was made to produce offspring up to three generations, so that the heterozygosity equilibrium was not yet attained. At G₃, the highest gene proportion was reached at 56% of C, followed by 31% of Y and 13% of H, while at G₃', the order was Y, C and H.

Jumping activity as a behavioral trait examined in

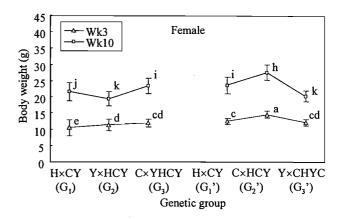


Figure 2. Mean body weight of female mice at rotational crossing at Wk3 and Wk10. Vertical lines represent standard deviation. Different letters among generations at each age indicate significant difference at p<0.05

this study is used as a measure of vigor in mice. It is a fact of nature that the main force responsible for selection is survival of the fittest in a particular environment, and only the vigorous and stronger animals can survive in that environment. In the wild state, and even in domesticated animals to a certain extent, there is a tendency towards an elimination of detrimental genes in order to achieve the survival of the fittest.

Utilization of heterosis is only one of the advantages that can be associated with some forms of crossbreeding. Heterosis that is often noticed in the resulting progeny, may lead to the production of individuals having characters more extreme than those in individuals resulting from any other method of breeding. Bell (1982) pointed out that when considering heterosis, it is necessary to recognize that some quantitative traits are highly heterotic; others are

Table 5. Heterosis effects for jumping height at Wk6

Genetic	Generation	Heterosis at		Heterosis at		
group	(G)	male		female		
		Unit	%	Unit	%	
$H \times CY$	1	6.27**	55.34	8.87**	80.42	
$Y \times HCY$	2	8.17**	72.11	7.07**	64.10	
$C \times YHCY$	3	8.97**	79.17	6.78**	61.53	
Pooled I		8.47**	74.75	10.50**	77.27	
$H \times YC$	1'	8.87**	78.29	9.47**	85.86	
$C \times HYC$	2'	6.17**	54.46	6.07**	55.03	
$Y \times CHYC$	3'	7.08**	62.49	5.27**	47.79	
Pooled II		7.37**	65.05	7.40**	67.27	

Heterosis unit, $h = [average of rotational crossbred - average of initial parental types]; <math>h\% = (h / average of initial parental types) \times 100$.

^{**} Significant at p<0.01.

7.65

Wk1 Wk3 Wk6 Genetic group Generation Wk10 (G) Unit % Unit % Unit % Unit % Male **H**×CY 0.82** 1.28** 2.16** 1 18.06 12.36 2.19** 9.47 8.19 0.93** $Y \times HCY$ 2 20.04 1.25** 12.07 -1.75** -7.65-1.86** -6.94 $C \times YHCY$ 3 0.75** 16.52 3.11** 30.78 3.78** 3.72** 16.56 13.91 Pooled I 0.83** 18.19 1.88** 18.15 1.40** 6.13 1.35** 5.06 **H**×**Y**C 1' 0.81** 2.34** 2.91** 17.84 22.59 12.75 1.78** 6.66 2' 4.82** $C \times HYC$ 1.35** 29.69 46.52 7.83** 34.29 8.75** 32.70 0.44^{NS} $Y \times CHYC$ 3' 1.11** 16.79 2.43** 23.46 1.60** 7.02 1.66 1.09** Pooled II 24.07 3.20** 30.88 4.12** 18.02 13.72 3.66 Female -0.01^{NS} 0.71** 0.26* -0.54* $H \times CY$ 1 15.63 2.59 -0.07-2.431.13** 0.76** -1.96** $Y \times HCY$ 2 16.74 10.97 -10.28-2.60** -11.76 **C**×YHCY 3 0.58** 12.76 1.75** 17.28 1.50** 7.84 1.33** 6.04 0.68** 1.04** Pooled I 15.03 10.28 -0.16* -0.84-0.60** -2.72 **H**×**Y**C 1' 0.71** 15.63 2.29** 22.60 1.91** 9.98 1.47** 6.67 2, 2.14** 47.25 4.40** 4.91** $C \times HYC$ 43.39 25.69 5.44** 24.64 0.99** 3' 1.90** -1.42** $Y \times CHYC$ 21.82 18.75 -7.45-1.84** -8.30Pooled II 1.28** 28.35 2.87** 28.40 1.80** 9.26 1.69**

Table 6. Heterosis effects for body weight at Wk1, Wk3, Wk6 and Wk10

midly heterotic, and still others show little or no heterosis. Heterosis level attained by rotational crossing may be less than when F1 females are used, and females by certain sire breeds may not be ideal with respect to maternal performance (Dickerson, 1969).

The highly significant and positive heterosis effects on jumping height have been indicated (table 5). As pointed out by Pattie et al. (1990), heterosis has the greatest effects on fitness traits.

Fuller (1962) stated that no reason exists to believe that special sets of genes are assigned to control behavior traits. Dominance and epistasis (interaction between loci) are two possible genetic mechanisms that cause heterosis, however contribution of epistasis to heterosis in crosses between breeds of domestic animals is generally considered to be negligible (Falconer and Mackay, 1996).

Heterosis effects on body weight attained in the present study were various depending on the strain of sire used and the maternal effects at each generation. Crossing involved the Y sire in addition to smaller maternal effects of Y dam tended to result in small heterosis. The negative heterosis effects may be assumed to be no heterosis on the trait of interest. These results were in agreement with those of a two-way rotational crossing previous report on (Kurnianto et al., 2000b).

In an experiment comparing grading-up to Angus, Polled Hereford and Santa Gertrudis breeds with twoand three-breed rotational crossing of these breeds, Chapman et al. (1970) reported generally higher estimates of heterosis for preweaning traits in generation 2 of rotational crossing than in generation 1. Generation 1 involved the use of crossbred dams to produce all backcrosses and the three-breeds crosses. Further, the level of heterosis shown by the three-breed cross was generally higher than that shown by two-breed crosses. Generally, the three-breed rotational crossing showed a higher level heterosis for most postweaning characters than two-breed rotational crossing. On the basis of a review of experimental results evaluating rotational crossing in beef cattle, Gregory and Cundiff (1980) concluded that high levels of heterosis are sustained by rotational crossing systems. Probably, the level of heterosis sustained is proportional to heterozygosity relative to maximum of F₁.

REFERENCES

Bell, A. E. 1982. Selection for heterosis-results with laboratory and domestic animals. Proceedings of the 2nd World Congress Genetic Applied Livestock on Production. Madrid.

Chapman, H. D., T. M. Clyburn and W. C. Cormick. 1970. Grading, and two-and three-breed rotational crossing as systems for production of calves to weaning. J. Anim. Sci. 31:642-651.

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

Falconer, D. S and T. F. C. Mackay. 1996. Introduction to

^{**} Significant at p<0.01; * Significant at p<0.05; NS Non Significant (p>0.05).

- Quantitative Genetics. Fourth Edition. Longman.
- Fuller, J. L. 1962. The genetics of behavior. In: The Behavior of Domestic Animals (Ed. E. S. E. Hafez). The Williams & Wilkins Company.
- Gregory, K. E and L. V. Cundiff. 1980. Crossbreeding in beef cattle: evaluation of systems. J. Anim. Sci. 51:1224-1242.
- Kurnianto, E., A. Shinjo and D. Suga. 1997. Comparison of the three growth models for describing the growth patterns in wild and laboratory mice. J. Vet. Epidemiol. 1:49-55.
- 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. 2000a. The inheritance of jumping activity in reciprocal cross of two

- subspecies of mice. Asian-Aus. J. Anim. Sci. 13:733-738.
- Kurnianto, E., A. Shinjo and D. Suga. 2000b. Heterosis effects of body weight and jumping height in rotational crossing of two-subspecies of mice. Asian-Aus. J. Anim. Sci. 13:888-893.
- Lasley, J. F. 1978. Genetics of Improvement Livestock. Third Edition. Prentice-Hall of India.
- Neville, Jr. W. E., B. G. Mullinix, 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. Iniques and S. S. Mansjoer. 1990. Second Workshop in Animal Breeding on Use of Computer Programs in Animal Breeding. IPB- Australia Project, Bogor, Indonesia.
- SAS. 1990. SAS/STAT User's Guide. Vol 2, Version 6, Fourth Edition. SAS Institute Inc.
- 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.