MARDI Res. J. 23(1) (1995): 75–82

Breed additive and individual heterotic effects on the reproductive performance in three rabbit breeds

(Kesan aditif baka dan heterotik individu terhadap prestasi reproduktif tiga baka arnab)

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Key words: genetic effects, reproductive performance, rabbit breeds

Abstract

Data recorded on 457 litters, from a three-breed diallel experiment, were used to characterize the Californian, Rex and Local rabbits for reproductive traits. The traits investigated included litter size, litter and individual average weights and mortality at birth and weaning stages. Unlike the breed of dam rankings, the breed of sire rankings of Californian, Rex and Local were generally consistent with the rankings in breed direct additive effects for many of the traits studied. The Rex maternal additive effects for average weight at birth and the Local direct additive effects negatively affected almost all the traits investigated, except mortality at birth, and litter weight and litter size at weaning. The Californian maternal additive effects and the Rex direct additve effects significantly increased the litter weight at weaning. The Local direct additive effects significantly improved the postnatal survivality while the Californian ones depressed it. All the two-breed combinations of the three breeds displayed significant heterosis on at least one of the traits investigated. The average heterosis ranged from 0.02% to 12.69%. These results supported the view that crossbreeding could be an effective means of improving the reproductive traits under the present environmental conditions.

Abstrak

Data tentang 457 kelahiran daripada ujian dialel tiga baka telah digunakan untuk mencirikan baka arnab Californian, Rex dan Tempatan bagi ciri pembiakan. Ciri yang dikaji ialah saiz kelahiran, purata berat kelahiran dan individu, serta kadar kematian pada peringkat kelahiran dan cerai susu. Tidak seperti taraf baka induk, taraf baka induk jantan untuk Californian, Rex dan Tempatan pada amnya sejajar dengan taraf kesan terus tambah baka bagi kebanyakan ciri yang dikaji. Kesan keibuan tambah bagi Rex untuk purata berat kelahiran dan kesan terus tambah bagi Tempatan mempengaruhi kebanyakan ciri yang dikaji secara negatif, kecuali kadar kematian pada peringkat kelahiran, berat kelahiran dan saiz sekelahiran pada peringkat cerai susu. Kesan keibuan tambah bagi Californian dan kesan terus tambah bagi Rex meningkatkan berat sekelahiran pada peringkat cerai susu. Bagi ciri kemandirian pada kelahiran pula, kesan terus tambah Tempatan meningkatkannya manakala Californian menurunkannya. Kesemua kacukan

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antara dua baka bagi tiga baka yang dikaji menunjukkan heterosis yang ketara bagi sekurang-kurangnya satu daripada ciri-ciri yang dikaji. Purata heterosis berjulat antara 0.02% hingga 12.69%. Hasil daripada kajian ini menyokong pandangan bahawa pengacukan boleh dijadikan kaedah yang berkesan untuk meningkatkan pembiakan dalam keadaan persekitaran semasa.

Introduction

Commercial rabbit production requires highly productive does capable of producing large numbers of viable young at slaughtering. Opportunities abound for selection of appropriate breeds for specific production goals and conditions, as differences among breeds for reproductive performance exist (Lukefahr et al. 1983) and use of specific breeds in crossbreeding system has proven to be effective in improving economic traits (Maseoro 1982; Rochambeau 1988). Although there is a dearth of information on the performance of temperate rabbit breeds in the tropics, tropical rabbit production could benefit from better exploitation of breed differences in additive and heterotic effects. The objective of this study was to assess breed differences in reproductive traits and to estimate the crossbreeding genetic effects associated with these traits.

Materials and methods

Breeds

The Californian, Rex and Local rabbit breeds were used in this experiment. Both the Californian and Rex breeds which were originally imported from Australia and the United States of America, respectively, were purchased from local farms. The Local breed was from a purebred colony kept at the Animal House of Universiti Kebangsaan Malaysia, Bangi. The Californian and Local lines have a uniform white coat, with black spots at the extremities and on the nose for the Californian, while the Rex has a wide range of coats varying from black, castor or spotted to white. As foundation stock, 25 does and 5 bucks of each of the breeds, aged 3–5 months, were purchased from the farms practising only pure breeding under standard management.

Cross-sectional data were used to estimate the mature weights of the three breeds (SAS 1982) and the results are shown in *Table 1*. The Californian could be considered as a medium-sized breed while the Rex and the Local would be classified as small-sized breeds (Lebas et al. 1986).

Management of the animals

The experiment was carried out at the Rabbit Unit of the Malaysian Agricultural Research and Development Institute (MARDI), Serdang, Selangor. The duration of the study was from September 1990 to February 1992. Except for rainfall, the environmental attributes of the location were found to be consistently stable throughout the experiment. The experimental period was divided into three seasons based on rainfall pattern: September 1990 to March 1991, April 1991 to September 1991 and October 1991 to February 1992.

The rabbits were housed in a two-tier cage system with the first and second level at 45 cm and 95 cm above the floor, respectively. The rabbitry was an open type with the walls made of wire mesh and the roof made of galvanized zinc. The cemented floor was washed daily to remove droppings and urine. Water was made available through an automatic watering system. The animals were fed three types of feed according to their physiological status: the bucks and the non-nursing does were fed a pellet type breeder feed containing 5% crude fat and 19% crude protein, whereas a pellet type lactation feed containing 20% crude fat and 19.5% crude protein was provided for the nursing ones. Three or four weanlings were grouped in cages of 58.5 cm x 57.5 cm x 33.5 cm dimension, and fed a pellet type grower feed containing 20% crude fat and 18% protein.

Table 1. Mature weight and coat attributes of three breeds of rabbit

Breed	No.*	Mature weight (g)	Age (weeks)	Coat colour	Hair characteristics
Californian	48	3 774.4 ± 103.0	30 ± 4	Mainly white, ear and nose with black spots	Long, dense and coarse
Rex	49	2 529.6 ± 74.9	24 ± 2	Black, castor, spotted or white	Short and soft
Local	45	1 902.3 ± 64.4	20 ± 2	Uniformly white	Long, dense and coarse

*Number of animals used in the computation of mature weights

Table 2. Number of litters born and weaned per mating type

Breed of sire	Breed of dams			
	Californian	Rex	Local	Total
Californian	97(35)	40(6)	26(14)	163(55)
Rex	41(22)	88(20)	28(11)	157(53)
Local	36(17)	33(8)	68(30)	137(55)
Total	174(74)	161(34)	122(55)	457(163)

Values in brackets indicate number of litters weaned

To characterize the three breeds for reproductive traits through assessment of the genetic effects associated with crossbreeding, a diallel cross mating design was implemented. The experiment was run by mating each doe for the first time to a buck randomly chosen among the three breeds, the second and the third mates coming from the remaining two breeds. The does were bred four times during the experiment: two times within their own breed and once with each of the other two breeds, several bucks of the three breeds being maintained at the same time. A total of 215 purebred animals, produced from the parental stock, were used in a diallel cross mating to produce all possible two-breed crosses and purebreds of the Californian, Rex and Local breeds. Four hundred and fifty-seven two-breed crossed and purebred litters were produced to represent the nine genetic groups out of which 163 litters were weaned *(Table 2).*

According to the breeding plan, the does were transferred to the buck's cage for the first mating at the age of 5 months while the first service of the bucks was at 6 months. Does and bucks were allowed to stay together in the same cage for about 24 h. The does were palpated 14 days later to check for pregnancy. Does that were found not to be pregnant were immediately returned to the buck for mating until a service was observed. For the pregnant does, a plastic basket measuring 40 cm x 30 cm x 10 cm containing some shredded paper as nest building material, was placed in the cage on the 28th day. The doe was presented to the male on the 17th day following kindling. The young were weaned at 28 days of age and transferred to a grower facility.

The animals were given veterinary treatment for common diseases such as earmite, skin diseases, snuffle and intestinal diseases. However, they were culled if the symptoms persisted. Culling reasons also included mastitis, sore hocks and failure to conceive after three consecutive exposures to the male and death. In case of death of a nursing doe, fostering was practised within the breed of the doe. The replacement does or bucks were randomly chosen among the young of the appropriate genetic group. No artificial light-dark cycle was adopted.

Parameters measured

The traits recorded were litter size at birth, number of young born alive, number of young born dead, litter weight at birth, and litter size and weight at weaning. Records of traits associated with birth were taken within 24 h after kindling. From these data, four variables were calculated: mortality rate at birth, mortality rate at weaning, average weight at birth and average weight at weaning.

Statistical procedure

The following model adopted from Harvey (1987) was used to analyze the data: Model I: $Y_{ijklmn} = \mu + S_i + B_{j(i)} + D_k + (SD)_{ik} + (BD)_{j(i)k} + M_1 + P_m + E_{ijklmn}$, where Y_{ijklmn} = performance of the *n*th individual born in the *1*th season of the *m*th parity from the *k*th breed of dam and the *j*th sire of the *i*th breed; μ = overall mean; S_i = fixed effect of the *i*th breed of sire; D_k = fixed effect of the *k*th breed of dam; $(SD)_{ik}$ = interaction effect between the *i*th breed of sire and the *k*th breed of dam; $(BD)_{j(i)k}$ = interaction effects of the *k*th breed of dam with the *j*th sire nested within the *i*th breed of sire; M_1 = fixed effect of the *1*th season of birth; P_m = fixed effect of the *m*th parity; and E_{ijklmn} = random residual, normally distributed with mean 0 and variance σ^2_e.

Model II was used to estimate the direct and maternal additive effects, and individual heterosis was adopted from Robison et al. (1981). Model II: $Y_{ijk} = \mu + A_cK_c + A_rK_r + A_1K_1 + M_cK_c + M_rK_r + M_1K_1 + H_{cl}K_{cl} + H_{cr}K_{cr} + H_{lr}K_{lr} + P_i + S_j + E_{ijk}$, where Y_{ijk} = performance of the *k*th progeny crossbred or purebred from Californian, Rex on Local parents, born in the *j*th season from the *i*th parity; μ = overall mean; A_c, A_r, A_l = direct additive effect of Californian, Rex and Local, respectively; K_c, K_r, K_l = percentage of genes contributed by the Californian, Rex and Local breed, respectively; M_c, M_r, M_l = maternal effect of the Californian, Rex and Local breed, respectively; H_{cl}, H_{cr}, H_{lr} = direct heterosis effect obtained from Californian-Local, Californian-Rex and Local-Rex crosses, respectively; K_{cl}, K_{cr}, K_{lr} = percentage of loci in the individual with gene coming from Californian, Rex and Local and other from one of the other two breeds (*Table 3*); P_i = fixed effect of the *i*th parity and E_{ijk} = random residual, normally distributed with mean 0 and variance σ^2_e. The restriction $\sum A_i = \sum M_i = 0$ was imposed. The procedure General Linear Model (SAS 1982) was used for Model I while the procedure Regression (SAS 1982) was used in fitting Model II.

Results

Breed least square means

Breeds of sire ranking for litter size at birth (total born) showed that the Californian-sired progenies were born in litters with 1.1

Table 3. Coefficients for direct and maternal additive and heterotic effects

Breed group[+]	Direct additive			Maternal additive			Heterozygosity		
	Cal	Rex	Loc	Cal	Rex	Loc	Cal x Rex	Cal x Loc	Rex x Loc
Cal	1	0	0	1	0	0	0	0	0
Rex	0	1	0	0	1	0	0	0	0
Loc	0	0	1	0	0	1	0	0	0
Cal x Rex	0.5	0.5	0	0	1	0	1	0	0
Rex x Cal	0.5	0.5	0	1	0	0	1	0	0
Rex x Loc	0	0.5	0.5	0	0	1	0	0	1
Loc x Rex	0	0.5	0.5	0	1	0	0	0	1
Cal x Loc	0.5	0	0.5	0	0	1	0	1	0
Loc x Cal	0.5	0	0.5	1	0	0	0	1	0

[+]Breed of sire is identified by the first symbol of the cross; Cal = Californian, Loc = Local

Table 4. Least square means of breed of sire and breed of dam effects for reproductive traits

	No.[1]	Total born	Litter size at weaning[2]	Mortality (%)		Litter weight (g)		Av. weight (g)	
				At birth	At weaning	At birth	At weaning	At birth	At weaning
Breed of sire									
Californian	155	6.5a	1.4	14.1	55.6	306.1a	1 275.4	49.3	453.8a
Rex	154	5.7a	1.3	15.0	54.7	269.1b	1 422.0	49.1	425.7ab
Local	126	5.4b	1.5	17.1	49.9	248.5b	1 340.6	47.5	404.4b
Av. standard error		0.2	0.6	2.2	3.0	8.6	89.1	0.9	14.1
Breed of dam									
Californian	174	6.8a	1.7a	12.1	51.9b	316.3a	1 433.4a	48.7	457.8a
Rex	146	5.5b	0.9b	17.5	62.1a	260.9b	1 354.7ab	48.8	419.6b
Local	114	5.0b	1.5a	17.3	45.8b	234.4c	1 176.2b	48.7	394.3c
Av. standard error		0.2	0.5	2.2	3.0	8.3	91.8	1.0	13.8

Mean values in each column with different letters are different (p <0.05)
[1]Number of litters used in the analysis
[2]Calculated by taking into account all litters born

(p >0.05) more kits than the Local-sired ones, respectively *(Table 4)*. However, at weaning, no significant difference was found between the three breeds of sire for litter size. Similar results were found for mortality rates at birth and at weaning.

The Californian-sired litters were 37.0 g and 57.6 g heavier (p <0.05) at birth than the Rex and Local-sired litters, respectively. However, there was no difference between litters of the three breeds for kit average weight at birth. At weaning, there were differences in average body weight while no difference was observed between litters.

Rabbits with Californian dams were born in litters with 1.3 and 1.8 more kits (p <0.05) than those born with Rex and Local dams, respectively. At weaning, these differences were narrowed down to 0.8 (p <0.05) and 0.2 kit, respectively. The breeds of dam had similar mortality rate in progenies at birth while the Rex-reared litters incurred significantly greater loss during the nursing period. The Californian, Rex and Local dams weaned 42.5, 21.1 and 45.0% of their litters, respectively.

Breed of dams ranking in litter body weight at birth showed that litters with Californian dams were 55.3 g and 81.9 g heavier (p <0.05) than those with Rex and Local dams, respectively, although similar average body weights at birth were recorded for the three groups. Rex dams showed a larger effect of 26.5 g for litter weight at birth than Local dams. At weaning, ranking in litter body weight and average body weight were Californian, Rex and Local in descending order; however, the difference between Californian and Rex as well as that between Rex and Local-reared ones were not significant.

Breed additive effects

The Californian direct additive effects were positively significant for litter size, litter weight at birth and mortality at weaning, while those of the Local breed were negative (p <0.01) for the same traits (*Table 5*). The Rex and Local direct additive effects on average body weight at birth were opposed, the former increased it (+11.9 g) while the latter decreased it (–16.4 g). However, at the weaning stage, the direct additive effects on average weight at weaning disappeared for Rex while its direct additive effects on litter weight became significant. Only the Local direct additive effects persisted at weaning (–137.1 g).

Table 5. Direct and maternal additive effect on reproductive traits in Californian, Rex and Local rabbits

Additive effect	Total born	At birth			At weaning			
		Mortality (%)	Litter wt. (g)	Av. wt. (g)	Mortality (%)	Litter wt. (g)	Av. wt. (g)	Litter size
Direct								
Cal	1.61	1.20	73.76*	4.51	23.43**	–135.91	74.08	–0.42
Rex	0.89	2.23	49.29	11.87*	–0.62	426.55*	63.02	0.95
Local	–2.50**	–3.43	–123.06**	–16.38*	–22.81**	–290.63	–137.11**	–0.52
s.e.	0.49	4.03	49.71	7.12	8.32	217.67	50.73	0.52
Maternal								
Cal	0.83	1.47	31.10	0.52	3.55	338.60*	24.85	0.70
Rex	–1.14	–1.85	–51.29	–10.22*	–1.72	–290.94	–61.28	–0.74
Local	0.31	0.38	20.19	9.70*	5.27	–47.67	36.42	0.04
s.e.	0.49	4.03	44.36	6.86	7.86	203.24	41.38	0.43

Cal = Californian
s.e. = average standard error
*p <0.05
**p <0.01

The Rex maternal additive effects on average body weight at birth were negative (–10.2 g) and opposed to the Local ones (+9.7 g). These effects were no longer significant at weaning. However, the Californian had significant maternal additive effects on litter body weight at weaning.

All the combinations among the three breeds displayed significant heterosis on at least one of the traits investigated (*Table 6*). The Californian-Local crosses significantly increased the average body weight at weaning, while the Californian-Rex crosses not only had similar effects, but also reduced (p <0.05) the preweaning mortality. The Rex-Local combination positively affected the litter size (p <0.05) and the litter body weight at birth (p <0.01). Although crossbreds generally recorded better performance compared with their purebred counterparts, significant average heterosis was found only for litter body weight at birth and average body weight at weaning.

Discussion

Differences between breeds of sire in litter size at birth observed here could be related to that in quality and quantity of spermatozoa (Lukefahr et al. 1983), whereas the differences in litter size at weaning under a given environment could be dependent on the differences in transmitted viability (adaptability to this environment). Present results indicated that while the Local sire was at a disadvantage for the litter size at birth, its ranking was improved at the weaning stage. This suggests a better postnatal viability of Local-sired progenies, as shown by the ranking in direct additive effects on the mortality at weaning, which might also reflect their adaptability to local conditions. Conversely, the Californian rabbits seemed to transmit unfavourable genes for postnatal viability to their progenies.

Differences in litter size at birth between breeds of dam have been found to be positively correlated with the breed mature body weights (Hulot and Matheron 1979; Slawinski and Arias 1988a). Results reported here were in line with the previous ones, as the ranking of dam breeds in litter size at birth paralleled closely that of mature body weight. However, differences in prenatal viability cannot be ruled out as breed of dam effects for this trait included a genetic contribution via maternal chromosomes coupled with any maternal effects due to cytoplasmic inheritance and parental environment. At weaning, the Local dams made up for the differences existing at birth between her and the Californian dam,

Table 6. Direct heterotic effects on reproductive traits in Californian, Rex and Local crosses

	Total born	At birth			At weaning			
		Mortality (%)	Litter wt. (g)	Av. wt. (g)	Mortality (%)	Litter wt. (g)	Av. wt. (g)	Litter size
Californian x Local	0.40	–1.00	35.33	1.42	–9.76	12.83	52.22*	0.56
Californian x Red	0.02	–3.67	9.64	0.79	–12.24*	–107.30	69.01*	0.41
Rex x Local	0.96*	–2.39	49.06**	–2.15	–4.87	–15.32	3.59	0.51
Av. standard error	0.40	–2.35	17.22	1.95	6.25	198.59	32.77	0.33
Av. absolute value	0.46	4.66	31.34*	0.02	8.64	–36.59	52.94*	0.49
Heterosis (%)[+]	8.08	12.68	11.97	0.02	12.17	2.79	12.69	5.91

[+]Percentage of purebred means
*p <0.05, **p <0.01

suggesting differences in preweaning mortality. However, the data here suggested that the influence of the genetic component on the preweaning mortality was preponderant compared with that of the maternal one.

The differences between breeds of sire in litter body weight at birth recorded here could have been induced by the differences in litter size, as there was no significant difference in kit average body weight at birth. At the weaning stage, the differences in body average weight might have been masked by that of litter size, resulting in similar litter body weights between breeds of sire. The Rex breed was found to be equipped with genes that positively affected (p <0.05) the litter body weight at weaning while the average body weight at weaning was significantly reduced by the Local direct genes.

Like the sires, the dam breeds kindled rabbits which had similar average body weight at birth. However, differences in litter body weight persisted, which might be attributed to the differences in number of progenies born. The results shown in *Table 5* suggested that these differences were little affected by the maternal additive effects, as far as the three breeds investigated here under local environmental conditions are concerned. This is consistent with previous reports that the litter body weight at birth and breed mature weight (dependent on breed genetic make-up) were positively correlated (Hulot and Matheron 1979). Examination of breed of dam least square means for litter and average body weight, and litter size at weaning apparently revealed some incoherence, as the Californian dam which had litters of significantly greater size and heavier rabbits than both the Rex and Local dams failed to edge the Rex in litter body weight at weaning. This might arise from the fact that, in computing litter size at weaning, all the litters born were taken into account, including those without any survivor at weaning while only litters that survived until weaning were included in the computation of litter body weight at weaning. Again, little maternal effects seemed to be involved in breed of dam differences for these traits.

The heterotic effects were generally moderate and restricted to fewer traits: litter size and litter weight at birth, mortality and average body weight at weaning. The crossbred had better performance compared with their purebred counterparts, with an average weight at weaning of 52.9 g. The heterosis concerned here could be specific. Results reported here were comparable in magnitude with those reported by Slawinski and Arias (1988b) on Chinchilla and New Zealand White crosses.

Given the direct and maternal genetic effects and the heterosis displayed by the crosses, the Rex-Californian (the last breed being the dam) seemed to be the most promising simple cross, as far as the

reproductive traits are concerned under present environmental conditions. However, the superiority of the Californian dam over the Local one could be seriously undermined when the overall breed efficiency is taken into account. As the Californian dam lost more often its whole litters and consumed significantly more feed than did the Local dam (Sangare 1993), it is likely that the nutritional and financial costs of raising replacements and maintaining mature females would favour the Local dam. Therefore, the alternative of rearing a small and thrifty doe is very attractive, as breeding females are reported to constitute 40–70% of the whole population (Fitzhugh 1978), this could be an effective way to reduce the farm overall running costs. Introducing some Local genes to boost the progeny survival and efficiency in a synthetic breed could be envisaged, if that solution proved to be viable.

Findings from this study also illustrated the opposition between direct and maternal genetic effects in rabbits, which has been documented by Slawinski and Arias (1988a) and more generally in mammals (Legates 1972). It is interesting to note that the Rex breed as the dam exerted negative effects on all the traits investigated; similarly, the Local as the sire, except for postweaning viability. Compared with direct genetic effects, the maternal effects on reproductive traits were generally not important. Therefore, direct genetic effects could play an important role in differentiating between breeds of dam involved in this experiment. This also suggested that, among the breeds under investigation, the choice of the sire breed is important to improve reproductive traits. In general, the findings suggest that the Rex is not a suitable breed to be used as a dam line while the Local is not a preferred sire line given the present environmental conditions.

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Accepted for publication on 11 January 1995