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Comparison of lifetime performance in mice under crisscross, repeat hybrid male cross and random mating systems*

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Summary. Mating systems that capitalize on heterosis in dairy cattle are the criss-cross (CC), the repeat hybrid male cross (RHMC) and random mating within a synthetic population (SYN). When performance is determined solely by direct additive genetic and dominance genetic effects, expected performance under CC (averaged over four generations after F_1 generation), relative to that under RHMC (or SYN) is (59 G1 + 69 G2 + 82 H)/64 (G1 + G2 + H), where Gi is direct additive genetic effect of breed i and H is direct heterosis. Five CC, five RHMC and one SYN population of mice were prepared to test 533, 534 and 410 females, respectively for performance during lifetime (155 days after mating). Each female was pair-mated at day 42 with a male from the SYN population and the number of lactations during the lifetime (NL), total number (TN) and weight (TW in g) of young born alive during lifetime, total number (AN) and weight (AW in g) of young raised to weaning (18 days), and actual length of reproductive life (RL in days) were recorded. Observed performance averaged over four generations was, under CC, RHMC and SYN, 4.74, 4.62 and 4.56 for NL, 49.9, 48.2 and 48.8 for TN, 86.0, 83.6 and 85.1 g for TW, 47.5, 45.5 and 46.3 for AN, 512.1, 517.9 and 521.1 g for AW, and 120.0, 117.6 and 116.7 for RL, respectively. Heterosis due to the female (H) was 10, 30, 33, 34, 43 and 9% for NL, TN, TW, AN, AW and RL, respectively. Direct additive genetic values were estimated for each pair of lines involved with CC or RHMC. These values were used in the formula to calculate expected performance in each mating system. The ratio of CC to RHMC for the expected and observed performance was 1.01 and 1.01 for NL, 1.04 and 1.04 for TN, 1.04 and 1.03 for TW, 1.04 and 1.04 for AN, 1.05 and 0.99 for AW, and 1.01 and 1.02 for RL, respectively. The ratio of CC to SYN for the observed performance was 1.04 for NL, 1.02 for TN, 1.01 for TW, 1.03 for AN, 0.98 for AW, and 1.03 for RL. As expected, the observed mean performance under CC was slightly larger than that under RHMC or SYN.

Key words: Crossbreeding – Lifetime performance – Mating system – Mice

Introduction

When two parental breeds of animals are mated, the offspring (F_1) often show better performance than the mean of parental performance. This phenomenon, called heterosis, has been widely used in production systems of chicken and swine (Dickerson 1973). However, heterosis has not been effectively used in less prolific species such as dairy cattle because of the limitation of producing replacement females from the parental breeds. A crossbreeding system for dairy cattle that capitalizes on heterosis but has a self-propagating crossbred female population would overcome this limitation. The crisscross and repeat hybrid male cross are mating systems with these characteristics.

The crisscross using two breeds (CC) is a rotational mating system in which female crossbreds are mated with males whose breed alternates between generations (Johansson and Rendel 1968). Rotational mating systems with more than two breeds have been used in swine (Winters et al. 1935) and beef cattle (Gregory and Cundiff 1980). The repeat hybrid male cross mating system (RHMC) involves two breeds, and successive generations of female crossbreds are mated with F_1 hybrid males from the two breeds (Hickman 1979). This mating system has been used experimentally in dairy cattle (McAllister et al. 1980). Random mating within a synthetic

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population (SYN) is a common procedure when genes of multiple breeds are to be maintained. The expected performance in successive generations has been discussed theoretically for CC and SYN (Dickerson 1973) and for CC and RHMC (Nagai and McAllister 1982). However, these mating systems have not been compared experimentally.

The purpose of the present study was to compare lifetime performance in mice under the three mating systems. Lifetime performance and its heterosis in mice have been described for cases of standardized litter size (Nagai et al. 1980) and no standardization of litter size (Nagai et al. 1984).

Materials and methods

Mice

Six straightbred lines of mice were developed in two populations (designated as P and Q) of different origin. They were M_P and M_Q, W_P and W_Q, and C_P and C_Q. Breeding history of these lines has been described by Nagai et al. (1978). Briefly, the P population was synthesized from four inbred strains, C3H/He, C57BL/6J, SWR/J and CBA/J, in 1966 while the Q population, introduced to Ottawa in 1971 from Lacombe, Canada (Dr. J. Newman), is a synthetic from the IC and OC random-bred strains maintained by Dr. D. Falconer, Edinburgh. Selection was conducted for 20 generations in M lines to increase postnatal maternal performance, as measured by 12-day body weights of a crossfostered first litter, and in W lines to increase adult body weight, as measured by individual body weight at 42 days in the first litter. Control lines (C) were maintained unselected for 20 generations. Calculated inbreeding coefficients for the C lines were approximately 13 percent. Using the selected lines (M_P, W_P, M_Q and W_Q), matings were made as follows: W_P(male)$\times M_P$(female), $M_Q \times M_P$, $W_Q \times M_P$, $M_Q \times W_P$, $W_Q \times W_P$, and $W_Q \times M_Q$. Resulting F_1 progeny were randomly mated to form one synthetic line, S, which was randomly bred for four generations before it was used for the present experiment. This procedure should reduce linkage disequilibrium.

The six straightbred lines were used to produce straightbreds, and F_1 males and females to set up lines under three mating systems. (Table 1): crisscross (CC), repeat hybrid male cross (RHMC) and random mating within the synthetic line (SYN). In CC and RHMC, five crosslines were produced using the six straightbred lines of different populations (P and Q). To produce the five crosslines each in CC and RHMC, the same combination of straightbred lines was made. Line-of-male alternated every generation in each crossline under CC. The F_1 males were used for mating consistently but reciprocal F_1 males alternated every generation under RHMC. Random mating was conducted in each of the six straightbred (STR) and synthetic lines (SYN). A total of 17 lines (straightbred lines and cross lines) were maintained under the above defined mating systems for six generations.

In each line of the CC, RHMC and STR, about 52 females were used for mating every generation. These females were divided into two groups, I and II. They were pair-mated with either males of their lines (group I) or males from the synthetic line (group II). Basically, two full sisters born to a pair in group I at the previous generation were divided into groups I and II at the next generation. In the synthetic line, about 104 pairs were mated randomly every generation, with the exception of avoiding full sib mating. Replacement females (breeders for the next generation) in each line were sampled from the sixth or seventh parity of group I females. Data on lifetime performance traits from group II of CC and RHMC, and from SYN were analyzed.

At each of the six generations, females 42 days old were pair-mated with slightly older males and maintained continuously for 155 days, allowing successive production of litters. The assumption was made that the results obtained for

Table 1. Mouse lines under different mating systems

Mating system	Line	Generation[a] 1 Male		1 Female	2 Male		2 Female
Crisscross (CC)	1)	M_Q	×	M_P	M_P	×	F_1 ($M_Q M_P$)[b]
	2)	M_P	×	M_Q	M_Q	×	F_1 ($M_P M_Q$)
	3)	W_P	×	W_Q	W_Q	×	F_1 ($W_P W_Q$)
	4)	C_P	×	C_Q	C_Q	×	F_1 ($C_P C_Q$)
	5)	M_P	×	W_P	W_P	×	F_1 ($M_P W_P$)
Repeat hybrid male cross (RHMC)	1)	F_1 ($M_Q M_P$)	×	F_1 ($M_P M_Q$)	F_1 ($M_P M_Q$)	×	F_2 (M_P, M_Q)
	2)	F_1 ($M_P M_Q$)	×	F_1 ($M_Q M_P$)	F_1 ($M_Q M_P$)	×	F_2 (M_Q, M_P)
	3)	F_1 ($W_P W_Q$)	×	F_1 ($W_Q W_P$)	F_1 ($W_Q W_P$)	×	F_2 (W_Q, W_P)
	4)	F_1 ($C_P C_Q$)	×	F_1 ($C_Q C_P$)	F_1 ($C_Q C_P$)	×	F_2 (C_Q, C_P)
	5)	F_1 ($M_P W_P$)	×	F_1 ($W_P M_P$)	F_1 ($W_P M_P$)	×	F_2 (W_P, M_P)
Straightbred (STR)	1)	M_P 2) W_P 3) M_Q			(e.g.) $M_P \times M_P$		
	4)	W_Q 5) C_P 6) C_Q					
Synthetic (SYN)	1)	S (M_P, W_P, M_Q, W_Q)			S (M_P, W_P, M_Q, W_Q)		

[a] This table shows the mating of the first two of the six generations tested

[b] F_1 ($M_Q M_P$) indicates F_1 cross of M_Q sire and M_P dam. Each line contained group I (using males and females as indicated) and group II (using SYN males mated with females shown)

this intensive (continual) breeding scheme would give the same ranking for a conventional scheme where females were exposed to males following weaning of their litter, i.e., no genotype×environment interaction. Litter size was not standardized and all young born alive were left with the mother until day 18 when the young were destroyed. Many pairs of mice used in the previous experiment (Nagai et al. 1980) were still reproducing up to 155 days after mating, and performance shown during 155 days of reproduction was defined as lifetime performance. Throughout this experiment, a commercial pellet feed (Purina Mouse Chow) and tap water were supplied ad libitum. Temperature and humidity in mouse rooms ranged from 20° to 24 °C and 40% to 50%, respectively.

Measurement

The following traits of lifetime performance were recorded for each female: number of parturitions during the 155-day period, total number of young born alive, total body weight of young born alive, total number of young weaned at day 18, total body weight of young at day 18 and days from mating (day 42) to the last parturition (length of reproductive life). The mean performance was calculated every generation for group II in each line under CC, RHMC and STR, and for SYN.

Genetic expectation of the comparison

Expected performance in a population has been given for CC and SYN (Dickerson 1973) and for CC and RHMC (Nagai and McAllister 1980). When performance of crosses from two parental breeds (strains) is determined by direct additive genetic effects and dominance genetic effects, and the amount of direct heterosis due to dominance effects is proportional to the number of heterozygous loci, performance under RHMC and SYN is expected to be constant after F_1 generation as follows:

$$(A+B+H)/2$$

where A and B are direct additive genetic effect of parental breeds 1 and 2 and H is the deviation of performance of F_1 cross from the mean performance of the two parental breeds.

Under CC (rotational crossbreeding using two sire breeds), F_1 females may be mated with males of breed 2 whose direct additive genetic effect is B. Performance of crosses at the next four generations after F_1 generation is

Table 2. Mean lifetime performance of mice under crisscross (CC) and random (SYN) matings

Trait	Generation	Line under CC 1	2	3	4	5	Mean[a]	SYN[a]	CC mean/SYN	Range
No. of parturitions during 155 days	3	5.21	4.83	3.57	4.60	4.36	4.51	4.40	1.03	
	4	4.63	5.03	4.52	5.10	3.53	4.57	4.24	1.08	
	5	4.85	4.54	4.50	4.90	4.25	4.61	4.59	1.00	1.01–1.07[b]
	6	4.63	5.37	4.85	5.62	4.80	5.25	4.99	1.05	
	Mean	4.83	4.94	4.36	5.06	4.24	4.74	4.56	1.04	0.94–1.13[c]
Total no. of young born alive	3	54.5	52.8	37.9	46.8	41.6	46.7	46.8	1.00	
	4	53.6	56.6	47.7	52.8	35.9	49.3	45.7	1.08	
	5	53.0	52.0	50.2	53.8	45.4	50.9	49.6	1.03	0.99–1.06
	6	51.9	59.2	50.9	55.2	46.1	52.7	52.9	1.00	
	Mean	53.3	55.2	46.7	52.2	42.3	49.9	48.8	1.02	0.91–1.13
Total wt. of young born alive (g)	3	90.3	90.6	67.5	78.4	74.0	80.2	81.4	0.99	
	4	93.2	97.1	85.4	88.4	60.8	85.0	79.3	1.07	
	5	90.8	92.2	89.1	88.7	77.7	87.7	87.8	1.00	0.98–1.04
	6	90.5	101.0	92.4	94.2	77.6	91.1	91.8	0.99	
	Mean	91.2	95.2	83.6	87.4	72.5	86.0	85.1	1.01	0.91–1.11
Total no. of young at day 18	3	52.4	51.0	34.5	43.3	39.0	44.0	44.1	1.00	
	4	52.4	53.7	45.2	50.2	33.4	47.0	43.6	1.08	
	5	49.7	51.1	48.2	50.5	42.1	48.3	47.3	1.02	0.99–1.06
	6	50.3	56.6	48.4	53.3	44.0	50.5	50.3	1.00	
	Mean	51.2	53.1	44.1	49.3	39.6	47.5	46.3	1.03	0.91–1.14
Total wt. of young at day 18 (g)	3	576.2	587.3	391.3	471.6	421.1	489.5	516.4	0.95	
	4	585.8	617.8	492.3	518.3	376.5	518.1	486.6	1.06	
	5	541.2	574.3	516.6	509.5	415.1	511.3	540.3	0.95	0.95–1.02
	6	553.8	585.7	517.0	538.0	453.6	529.6	541.0	0.98	
	Mean	564.3	591.3	479.3	509.4	416.6	512.1	521.1	0.98	0.88–1.08
Days of reproductive life	3	123.9	127.0	125.2	119.0	109.8	121.0	116.7	1.04	
	4	124.8	128.0	113.2	120.8	93.6	116.1	109.0	1.07	
	5	117.0	128.2	117.8	118.2	110.5	118.3	117.1	1.01	1.00–1.06
	6	122.3	130.2	118.8	133.9	117.0	124.4	123.8	1.00	
	Mean	122.0	128.4	118.8	123.0	107.7	120.0	116.7	1.03	0.94–1.11

[a] Number of females tested at generations 3, 4, 5 and 6 was 118, 135, 140 and 140 under CC, and 104, 104, 100 and 102 under SYN
[b] Range of the ratio using overall means
[c] Range of the ratio using means for a line-generation (for explanation, see text)

expected to be as follows:

$(A+3B)/4+H/2$

$(5A+3B)/8+3H/4$

$(5A+11B)/16+5H/8$

$(21A+11B)/32+11H/16.$

Therefore, the mean performance of crosses over the four generations is

$(59A+69B)/128+41H/64.$

The ratio of the performance under CC to performance under RHMC (or SYN) averaged over the four generations is

$(59A+69B+82H)/64\,(A+B+H).$

Of course, the composition of RHMC starting with a backcross to A instead of B would give the same results as above replacing A by B, and vice versa.

Data were recorded from generations 3 to 6 for CC, STR and SYN, and from contemporaneous generations 2 to 5 for RHMC. Lifetime performance averaged over four generations under STR (as shown in Table 4) was used to estimate direct additive genetic effects, A and B, in the above formula. Heterosis, expressed as the deviation of performance of F_1 cross from parental (straightbred) lines, was calculated using data on generation 1 under RHMC and STR (Nagai et al. 1984).

Range of the ratio of the observed mean performance, CC/RHMC (or CC/SYN)

Variance for each trait was calculated for each generation in each line. The variance was averaged over generations and lines within the mating system, i.e., CC, RHMC or SYN. The mean variance divided by the mean number of females per generation by line was square-rooted for each trait to obtain approximate standard error (S.E.) of the mean for a line-generation. The approximate standard error was divided by

Table 3. Mean lifetime performance of mice under repeat hybrid male cross (RHMC) mating

Trait	Generation	Line under RHMC					Mean[a]	CC mean/ RHMC mean	Range
		1	2	3	4	5			
No. of parturitions during 155 days	2[b]	5.16	4.29	4.40	5.29	4.52	4.73	0.95	
	3	4.28	4.67	3.83	4.80	5.27	4.57	1.00	
	4	4.37	5.04	4.67	5.20	4.50	4.76	0.97	1.00–1.05[c]
	5	4.63	4.31	3.80	4.97	4.37	4.42	1.19	
	Mean	4.61	4.58	4.18	5.07	4.67	4.62	1.03	0.90–1.16[d]
Total no. of young born alive	2	58.0	48.1	47.4	53.9	41.9	49.9	0.94	
	3	45.8	49.3	41.7	48.3	49.0	46.8	1.05	
	4	47.4	56.2	48.9	54.4	46.3	50.6	1.01	1.00–1.07
	5	47.9	48.8	40.4	48.6	42.5	45.6	1.16	
	Mean	49.8	50.6	44.6	51.3	44.9	48.2	1.04	0.89–1.19
Total wt. of young born alive (g)	2	99.5	84.0	84.3	94.1	72.1	86.8	0.92	
	3	80.6	84.7	73.1	82.6	84.2	81.0	0.95	
	4	80.9	94.9	89.4	93.8	77.9	87.4	1.00	1.00–1.06
	5	83.9	82.9	71.0	84.2	73.1	79.0	1.15	
	Mean	86.2	86.6	79.5	88.7	78.8	83.6	1.03	0.89–1.17
Total no. of young at day 18	2	56.0	46.1	45.0	52.0	35.4	46.9	0.94	
	3	43.6	48.0	40.0	44.6	45.5	44.3	1.06	
	4	43.7	54.5	47.0	51.5	41.1	47.6	1.01	1.01–1.08
	5	46.0	45.8	39.2	45.7	38.3	43.0	1.17	
	Mean	47.3	48.6	42.8	48.5	40.1	45.5	1.04	0.89–1.22
Total wt. of young at day 18 (g)	2	644.5	559.3	531.4	583.1	400.4	543.7	0.90	
	3	522.1	555.2	447.4	494.8	533.9	510.7	1.01	
	4	498.5	615.6	552.9	574.6	452.3	538.8	0.95	0.96–1.02
	5	527.7	506.0	447.3	501.1	409.3	478.4	1.11	
	Mean	548.2	559.0	494.8	538.4	449.0	517.9	0.99	0.85–1.14
Days of reproductive life	2	127.8	113.5	115.9	130.9	112.1	120.0	1.01	
	3	106.3	120.9	106.4	125.9	121.4	116.2	1.00	
	4	118.4	125.7	122.6	125.5	109.9	120.4	0.98	1.00–1.05
	5	120.1	119.9	103.0	118.0	107.3	113.7	1.09	
	Mean	118.2	120.0	112.0	125.1	112.7	117.6	1.02	0.91–1.14

[a] Number of females tested was 123, 120, 145 and 146 at generations 2, 3, 4 and 5, respectively
[b] Generation 2 under RHMC is contemporaneous with generation 3 under CC period
[c] Range of the ratio using overall means
[d] Range of the ratio using means for a line-generation

Table 4. Mean lifetime performance of straightbred lines of female mice pair-mated with males from line S

Trait	Generation	Line					
		M_P	M_Q	W_P	W_Q	C_P	C_Q
No. of parturitions during 155 days	3	4.61	3.45	3.95	3.10	4.17	4.75
	4	5.63	4.22	4.25	3.54	5.24	5.35
	5	4.73	4.12	4.32	4.48	4.96	4.83
	6	5.04	4.36	4.85	3.56	5.47	4.58
	Mean	5.00	4.04	4.34	3.67	4.96	4.88
Total no. of young born alive	3	42.4	39.6	39.3	34.6	38.3	54.5
	4	55.7	49.2	41.7	40.2	50.3	61.7
	5	46.5	41.8	39.8	49.1	49.3	57.0
	6	47.2	47.2	43.1	38.5	47.0	46.3
	Mean	48.0	44.5	41.0	40.6	46.2	54.9
Total wt. of young born alive (g)	3	69.6	70.2	69.9	59.4	62.6	91.1
	4	92.6	88.4	74.1	70.2	82.1	104.1
	5	77.2	74.5	70.0	85.9	81.6	97.1
	6	77.8	83.3	76.5	66.3	78.9	80.1
	Mean	79.3	79.1	72.6	70.5	76.3	93.1
Total no. of young at day 18	3	38.8	38.1	37.0	33.4	34.3	49.7
	4	52.0	47.8	36.9	38.8	45.8	58.1
	5	41.8	39.9	36.0	46.3	42.1	54.9
	6	44.6	45.7	40.8	36.6	42.9	44.7
	Mean	44.3	42.9	37.7	38.8	41.3	51.9
Total wt. of young at day 18 (g)	3	428.2	436.0	412.9	357.5	362.6	501.6
	4	575.5	556.6	406.2	448.5	461.9	600.0
	5	444.9	470.7	393.3	503.3	406.0	560.8
	6	499.6	497.5	436.6	386.5	410.9	474.4
	Mean	487.1	490.2	412.3	424.0	410.4	534.2
Days of reproductive life	3	117.3	92.2	105.3	94.0	99.5	116.6
	4	131.4	116.0	104.3	98.5	123.0	131.7
	5	110.2	115.9	109.6	116.3	121.7	122.5
	6	122.7	114.3	127.8	100.0	126.9	118.7
	Mean	120.4	109.5	111.8	102.2	117.8	122.4

Number of females tested over four generations ranged from 86 to 93 for the six lines

$\sqrt{20}$ for CC or RHMC, and by $\sqrt{4}$ for SYN to obtain approximate standard error of the overall mean under the respective mating system (e.g. CC). The t-test was used to test the significance of differences between the overall means. The total number of females tested (in group II) was 533, 534, 540 and 410 for CC, RHMC, STR and SYN, respectively, with about equal number of females per generation by line. To obtain a measure of variation in the ratio of the observed mean performance of a trait for CC/RHMC, for example, the following were calculated:

$$\frac{(\text{Mean} - \text{S.E.})_{CC}}{(\text{Mean} + \text{S.E.})_{RHMC}} \text{ to } \frac{(\text{Mean} + \text{S.E.})_{CC}}{(\text{Mean} - \text{S.E.})_{RHMC}}.$$

Results

Mean lifetime performance under crisscross (CC) and random (SYN) matings, classified by generation and line, is shown in Table 2. Lifetime performance, averaged over lines and generations, was generally larger under CC than under SYN. The ratio of the lifetime performance averaged over the five lines under CC to the lifetime performance under SYN (next to the right column in Table 2) ranged from 0.95 (for total body weight of young at day 18 at generations 3 and 5) to 1.06 (for number of parturitions during 155 days at generation 4). The range of the ratios for means representative of a line-generation was generally narrow: 0.88 to 1.08 for the total weight of young at day 18, for example (right column in Table 2). The ratio for overall means ranged from 0.95 to 1.02 (right column in Table 2). The difference between the overall means was not statistically significant.

Mean lifetime performance under repeat hybrid male cross (RHMC), classified by generation and crossline, is shown in Table 3. Lifetime performance under RHMC, when averaged over five lines, was fairly constant for the four generations examined. The ratio of CC to RHMC for mean lifetime performance (next to the right column in Table 3) ranged from 0.90 (for total body weight of young at day 18 at generation 2) to 1.19 (for number of parturitions during 155 days at generation 5). In general, the range of the ratios for means representative of a line-generation was narrow: 0.89 to 1.19 for total number of young born alive, for example (right column in Table 3).

Mean lifetime performance for the six straightbred lines, (STR) classified by line and generation, is shown in Table 4. Performance averaged over four generations varied among the six lines. This is due to the different genetic backgrounds of the populations (P and Q) and selection conducted to increase postnatal maternal performance in M_P and M_Q and to increase adult weight in W_P and W_Q (Nagai et al. 1978). Based on the average performance, direct additive genetic effect was estimated for each pair of straightbred lines that were involved in CC and RHMC crosslines (coded 1, 2, 3, 4 and 5). Percentage heterosis estimated from straightbreds and their F_1's (Nagai et al. 1984) was used to obtain the approximate size of direct heterosis (right column in Table 5). Applying the values of direct additive genetic effects and direct heterosis to the formula presented previously, expected mean performance was calculated for each of the five crosslines under CC and RHMC (Table 6). The ratio (CC/RHMC) for the expected mean performance ranged from 0.99 to 1.06 (next to the right column in Table 6), whereas the ratio (CC/RHMC) for the observed performance (Tables 2

Table 5. Mean lifetime performance of straightbred lines 1 and 2 used for crisscross (CC) or repeat hybrid male cross (RHMC) mating and the magnitude of heterosis

Trait	CC or RHMC line	Straightbred line		Heterosis
		1	2	
No. of parturitions during 155 days	1	4.04	5.00	0.63 (14)[a]
	2	5.00	4.04	0.63 (14)
	3	4.34	3.67	0.56 (14)
	4	4.96	4.88	0.44 (9)
	5	5.00	4.34	0 (0)
	Mean	4.67	4.39	0.45 (10)
Total no. of young born alive	1	44.5	48.0	17.1 (37)
	2	48.0	44.5	17.1 (37)
	3	41.0	40.6	11.4 (28)
	4	46.2	54.9	13.1 (26)
	5	48.0	41.0	8.9 (20)
	Mean	45.5	45.8	13.7 (30)
Total wt. of young born alive (g)	1	79.1	79.3	32.5 (41)
	2	79.3	79.1	32.5 (41)
	3	72.6	70.5	20.0 (28)
	4	76.3	93.1	24.6 (29)
	5	79.3	72.6	18.2 (24)
	Mean	77.3	78.9	25.8 (33)
Total no. of young at day 18	1	42.9	44.3	17.4 (40)
	2	44.3	42.9	17.4 (40)
	3	37.7	38.8	13.0 (34)
	4	41.3	51.9	15.4 (33)
	5	44.3	37.7	9.4 (23)
	Mean	42.1	43.1	14.5 (34)
Total wt. of young at day 18 (g)	1	490.2	487.1	224.8 (46)
	2	487.1	490.2	224.8 (46)
	3	412.3	424.0	196.5 (47)
	4	410.4	534.2	212.5 (45)
	5	487.1	412.3	143.9 (32)
	Mean	457.4	469.6	199.3 (43)
Days of reproductive life	1	109.5	120.4	16.1 (14)
	2	120.4	109.5	16.1 (14)
	3	111.8	102.2	11.8 (11)
	4	117.8	122.4	8.4 (7)
	5	120.4	111.8	−2.3 (−2)
	Mean	116.0	113.3	10.3 (9)

[a] Heterosis in %, taken from Nagai and McAllister (1983)

Table 6. Expected mean lifetime performance[a] of mice under crisscross (CC) and repeat hybrid male cross (RHMC) matings

Trait	CC or RHMC line	Expected performance		CC/RHMC	
		CC	RHMC	Expected	Observed
No. of parturitions during 155 days	1	4.96	4.84	1.02	1.05
	2	4.89	4.84	1.01	1.08
	3	4.34	4.29	1.01	1.04
	4	5.20	5.14	1.01	1.00
	5	4.64	4.67	0.99	0.91
	Mean	4.81	4.76	1.01	1.01
Total no. of young born alive	1	57.3	54.8	1.05	1.07
	2	57.1	54.8	1.04	1.09
	3	48.1	46.5	1.03	1.05
	4	59.3	57.1	1.04	1.02
	5	49.9	49.0	1.02	0.94
	Mean	54.3	52.4	1.04	1.04
Total wt. of young born alive (g)	1	100.0	95.5	1.05	1.06
	2	100.1	95.5	1.05	1.10
	3	84.3	81.6	1.04	1.05
	4	101.1	97.0	1.04	0.99
	5	87.3	85.1	1.03	0.92
	Mean	94.7	91.0	1.04	1.03
Total no. of young at day 18	1	54.8	52.3	1.05	1.08
	2	54.7	52.3	1.05	1.09
	3	46.6	44.8	1.04	1.03
	4	56.9	54.3	1.05	1.02
	5	46.8	45.7	1.02	0.99
	Mean	51.9	49.9	1.04	1.04
Total wt. of young at day 18 (g)	1	632.5	601.1	1.05	1.03
	2	632.8	601.1	1.05	1.06
	3	544.5	516.4	1.05	0.97
	4	613.3	578.6	1.06	0.95
	5	539.0	521.7	1.03	0.92
	Mean	591.7	563.2	1.05	0.99
Days of reproductive life	1	125.7	123.0	1.02	1.03
	2	124.8	123.0	1.01	1.07
	3	114.2	112.9	1.01	1.06
	4	125.7	124.3	1.01	0.98
	5	114.3	115.0	0.99	0.96
	Mean	121.1	119.8	1.01	1.02

[a] (59A + 69B + 82H)/128 for CC and (64A + 64B + 64H)/128 for RHMC. For A, B and H, see text

Table 7. The ratio of the expected performance to the observed under CC and RHMC mating

Trait	Mating	Line					Mean
		1	2	3	4	5	
No. of parturitions during 155 days	CC	1.03	0.99	1.00	1.03	1.09	1.01
	RHMC	1.05	1.06	1.03	1.01	1.00	1.03
Total no. of young born alive	CC	1.08	1.03	1.03	1.14	1.18	1.09
	RHMC	1.13	1.08	1.04	1.11	1.09	1.09
Total wt. of young born alive	CC	1.10	1.05	1.01	1.16	1.20	1.10
	RHMC	1.11	1.10	1.03	1.09	1.08	1.09
Total no. of young at day 18	CC	1.07	1.03	1.06	1.15	1.18	1.09
	RHMC	1.11	1.08	1.05	1.12	1.14	1.10
Total wt. of young at day 18	CC	1.12	1.07	1.14	1.20	1.29	1.15
	RHMC	1.10	1.08	1.04	1.07	1.16	1.09
Days of reproductive life	CC	1.03	0.97	0.96	1.02	1.06	1.01
	RHMC	1.04	1.03	1.01	0.99	1.02	1.02

and 3) ranged from 0.91 to 1.10. In general, the two ratios, expected and observed, were in good agreement, particularly when five crosslines of CC and RHMC were considered collectively, e.g., 1.01 vs. 1.01 for number of parturitions during 155 days.

Observed and expected performance were compared under CC (Tables 2 and 6) and also under RHMC (Tables 3 and 6). Relative to the observed performance averaged over four generations, expected mean performance was, in general, greater than the observed under both CC and RHMC. The ratio of the expected to the observed was larger than one in most cases (Table 7), e.g., 1.03 (4.96/4.83) for number of parturitions during 155 days in line 1 under CC.

The lifetime performance under SYN (Table 2) was similar to that under RHMC (Table 3), particularly when data were averaged over four generations (for SYN) and also five lines (for RHMC). The means (and standard deviations) under SYN, CC and RHMC were 4.56 (1.66), 4.74 (1.39) and 4.62 (1.61) for number of parturitions during 155 days, 48.8 (19.8), 49.9 (17.4) and 48.2 (19.3) for total number of young born alive, 85.1 (30.2), 86.0 (29.1) and 83.6 (29.8) for total weight of young born alive, 46.3 (19.8), 47.5 (17.4) and 45.5 (21.1) for total number of young at day 18, 521.1 (210.4), 512.1 (170.5) and 517.9 (214.3) for total weight of young at day 18 and 116.7 (37.4), 120.0 (30.4) and 117.6 (37.6) for days of reproductive life.

Discussion

Crossbreeding can capitalize on both additive genetic effects of superior breeds and heterosis due to non-additive genetic effects. Crisscross (CC) and repeat hybrid male cross (RHMC) are crossbreeding systems that can be practically used for dairy cattle. Genetic theory underlying these systems has been discussed (Nagai and McAllister 1982) but without experimental support. The mouse has a short generation interval and is less expensive to maintain than dairy cattle. Breeding principles transcend species (Roberts 1965). In the present study, lifetime performance under CC and RHMC was examined experimentally using various mouse lines with known breeding history. The mouse experiment should provide a guide for the use of CC and RHMC in dairy cattle experiments (McAllister et al. 1980) which require, at least, several decades, and substantial money and labor to obtain definite results.

The mean performance of the four generations examined was expected to be slightly greater under CC than under RHMC (Table 6). The expected ratio CC/RHMC was in good agreement with the observed ratio CC/RHMC in each of the five CC and RHMC lines (Table 6). The six straightbred lines varied in additive genetic effects and the six traits examined exhibited different degrees of heterosis (Table 5). The Holstein and Ayrshire-based lines used for RHMC and CC (McAllister et al. 1980) differ in breed additive genetic effects for a single annual milk yield by 20% and are expected to show 0–20% heterosis in various lifetimes performance traits. If genetic mechanisms underlying lifetime performance in dairy cattle are similar to those assumed in the mouse experiment, then the agreement of expected and observed ratios (CC/RHMC) may also be achieved in dairy cattle.

The ratio (CC/RHMC) for expected performance was in good agreement with the ratio (CC/RHMC) for observed performance, but expected performance was generally greater than observed performance under both CC and RHMC (Table 7). The discrepancy may be due to epistatic effects of genes that inflate estimates of dominance genetic effects from F_1 and parent data, making the size of heterosis expected from heterozygosity too large (Sheridan 1981; Kinghorn 1982). Whatever the genetic mechanisms for the discrepancy are, the evidence that observed performance was lower than the expected under both CC and RHMC (Table 7) led to the good agreement in the ratios CC/RHMC for observed and expected performance. Actual performance observed in various kinds of crossbreds (e.g. F_2) that is related to expected performance under different genetic models warrants further study.

Observed performance under SYN was similar to that under RHMC (Tables 2 and 3), particularly when performance was averaged over generations (under SYN) and also lines (under RHMC). When additive genetic effects and direct heterosis from heterozygosity are considered for two lines, performance under SYN and RHMC is expected to be equal and, after F_1 generation, constant within SYN or RHMC. In this study, the five RHMC crosslines were derived from six straightbred lines (M_P, M_Q, W_P, W_Q, C_P and C_Q), which also provided the major source of genes for the SYN line. Thus, the finding above would provide a fairly clear idea regarding the choice of SYN or RHMC systems in dairy cattle. The RHMC requires maintenance of two straightbred lines to produce F_1 bulls for mating with crossbred heifers (cows) while under SYN, bulls can be self-supplied from a synthetic population to which they belong. Superior additive genes resulting from selection of bulls can be transmitted more directly under SYN than under RHMC. Bulls do not need to be F_1's if they have normal libido and semen quality. For these reasons, it appears that SYN is a good alternative to RHMC, provided that unwanted genetic effects (e.g., inbreeding) can be avoided under SYN. Although the average performance over four generations was, in general, superior under CC than under SYN, the superiority was nominal. Considering that the performance under CC is expected to fluctuate over generations depending on males used for mating, use of CC also needs to be carefully planned. Holsteins dominate at least in Canada and USA and thus CC would begin with an F_1 female out of Holstein dams. Genetic mechanisms underlying performance would be more complex than those in mice. Dairy cattle breeding plans involving CC, RHMC and SYN need to be well investigated.

Lifetime performance in mice under continuous cohabitation is expressed jointly by females and their mates (Nagai et al. 1984). Therefore, the lifetime performance can not be compared between CC and RHMC without controlling males for mating. In the present study, all females were pair-mated with males of the same synthetic line, SYN, to permit a valid comparison between CC and RHMC. Sampling of males from line SYN may affect comparison of CC with RHMC at one generation. However, such sampling errors were expected to cancel out when data were pooled over four generations, as done in the present study.

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