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Expected Performance Under Repeated Hybrid Male Cross and Crisscross Mating Systems

J. Nagai and A. J. McAllister
Animal Research Centre, Agriculture Canada, Ottawa, Ontario (Canada)

Summary: The expected performance of two crossbreeding systems, the crisscross (CC) and repeated hybrid male cross (RHMC) was compared. These systems are of particular interest for less prolific species such as dairy cattle. Under the CC, the expected performance fluctuated over generations while under the RHMC, performance was constant after the F_1 generation. After a few generations of crossing, the ratio of the average performance of the two alternative CCs to the performance under RHMC approached $(6+4H)/(6+3H)$ where H was a coefficient indicating the degree of heterosis. When the parent breed difference (D) was small (10%) and heterosis (H) substantial (30%), the CC involving the first back cross to the superior sire breed was expected to exceed the RHMC by 6% after a few generations of crossing. The expected performance under CC and RHMC for various values of D and H was calculated.

Key words: Mating systems – Expected performance – Crossing

Introduction

The lower reproductive rate of dairy cattle compared to other species (e.g. swine and chicken) severely limits the effective use of F_1 hybrid superiority particularly when F_1 replacement females are produced from the parent lines. A crossbreeding system for dairy cattle that capitalizes on heterosis but which has a self-propagating crossbred female population would overcome this limitation. The crisscross (CC) and the repeat hybrid male cross (RHMC) are two systems with these characteristics.

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The crisscross (CC) is a rotational mating system involving two breeds (strains) 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 repeated hybrid male cross (RHMC) mating system 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 in dairy cattle (McAllister et al. 1980). The purpose of this paper was to predict the genetic components of performance for a single trait under these mating systems (CC and RHMC) without selection. Further they were to be evaluated for multiple-trait performance for overall merit such as for lifetime performance in dairy cattle.

Analytical Method and Results

It was assumed that 1) the breed mean is determined completely by additive direct and maternal genetic effects (g^I and g^M, respectively) and direct and maternal heterosis (h^I and h^M), and 2) a linear relation exists between percent heterozygosity and heterosis. Expected genetic performance when two breeds A and B are used under RHMC and CC is shown in Table 1. In RHMC, the additive direct genetic effect (g^I) is $(A+B)/2$ constantly while in CC, g^I approaches $(A+2B)/3$ or $(2A+B)/3$, depending on the breed of male that was used for mating at the last generation. Direct heterosis (h^I) is 50% after the second mating in RHMC while it approaches 67% in CC. For both CC and RHMC, the maternal genetic effects (g^M and h^M) at one generation are identical with those of the corresponding direct genetic effects from the previous generation.

The efficiency of various mating systems is determined mainly by the following factors (Dickerson 1973): 1) reproductive rate of the species, 2) magnitudes of heterosis and of loss of epistatic superiority of pure breeds, 3) size of breed differences in performance of purebreds, and 4) importance of interactions of genetic components with management or marketing systems.

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Table 1. Expected genetic components of performance under the repeated hybrid male cross (RHMC) and crisscross (CC) mating systems

Mating system	Sire	× Dam	g^I	h^h	g^M	h^M
RHMC	A	× B	(A+B)/2	(AB)	B	–
	$F_1(A \cdot B)$	× $F_1(A \cdot B)$	(A+B)/2	(AB)/2	(A+B)/2	(AB)
	$F_1(A \cdot B)$	× $F_2(A \cdot B)$	(A+B)/2	(AB)/2	(A+B)/2	(AB)/2
	$F_1(A \cdot B)$	× $F_1(A \cdot B)F_2(A \cdot B)$	(A+B)/2	(AB)/2	(A+B)/2	(AB)/2
		⋮				
	$F_1(A \cdot B)$		(A+B)/2	(AB)/2	(A+B)/2	(AB)/2
CC	A	× B	(A+B)/2	(AB)	B	–
	B	× $F_1(A \cdot B)$	(A+3B)/4	(AB)/2	(A+B)/2	(AB)
	A	× $B \cdot F_1(A \cdot B)$	(5A+3B)/8	3(AB)/4	(A+3B)/4	(AB)/2
	B	× $A \cdot B \cdot F_1(A \cdot B)$	(5A+11B)/16	5(AB)/8	(5A+3B)/8	3(AB)/4
	A	× $B \cdot A \cdot B \cdot F_1(A \cdot B)$	(21A+11B)/32	11(AB)/16	(5A+11B)/16	5(AB)/8
	B	× $A \cdot B \cdot A \cdot B \cdot F_1(A \cdot B)$	(21A+43B)/64	21(AB)/32	(21A+11B)/32	11(AB)/16
		⋮				
	B		(A+2B)/3	2(AB)/3	(A+2B)/3	2(AB)/3

A and B represent two breeds used for crossing; g^I and g^M represent additive direct and maternal genetic effects, respectively while h^I and h^M represent direct and maternal heterosis, respectively.

To examine the effects of heterosis and the difference of performance between two breeds on the expected performance of crossbreds of the CC and RHMC systems the following conditions were considered: 1) the expected performance is determined only by additive direct genetic effects and direct heterosis, 2) two breeds A and B have relative performance 1 and 1-D respectively, where D is the difference in performance between the two breeds ($O \leqq D \leqq 1$), and 3) heterosis is measured as the deviation from the average performance of two parental breeds, i. e., H(2-D)/2 where H is a negative or positive coefficient indicating the degree of heterosis. Since either sire breed (A or B) may be used to mate the F_1 female crossbred population (A × B), two types of CC are possible; CC-1, a backcross to the superior sire breed first and CC-2, a backcross to the inferior sire breed first.

The relative performance of crosses under the RHMC and the CC systems was calculated for several combinations of values of D and H of 0.1, 0.3, and 0.5 (Fig. 1). When the difference between the parent lines is large relative to the degree of heterosis (D=0.5, H=0.1), the performance of the superior breed exceeds that of the RHMC and of both the CC crosses. When heterosis is large relative to the difference between the parent lines (D=0.1, H=0.5), the RHMC and CC crosses are all superior to the better parent breed. The performance of the superior breed is close to that of the crosses under the RHMC and CC-1 when D=0.1 and H=0.1. For moderate levels of a difference between parent breeds and heterosis (D=0.3, H=0.3) the performance of the superior parent breed is slightly above the RHMC cross but below that of the CC-1 cross. As the parent breed differences and heterosis become large (D=0.5, H=0.5) the difference of the RHMC and CC-1 crosses becomes larger about the superior parent breed mean.

The performance of the CC-1 cross relative to the RHMC for all possible combinations of D and H of 0.1, 0.2, and 0.3 is shown in Table 2. At generation 6, the CC-1 has about a 2% advantage over the RHMC for each 0.1 increase in the parent breed difference (D) for a given level of heterosis (H). The advantage for a 0.1 increase in heterosis for a given level of parent breed difference is only about 1%. The RHMC cross exceeds the CC-1 only slightly in alternate generations when D=0.2, H=0.1 or D=0.3 and H=0.1 or 0.2. For the various D and H combinations calculated the advantage of CC-1 over RHMC at generation 6 ranges from 3 to 9%.

When D is small (e.g. D=0.1) and H is substantial (e.g. H=0.3), the expected performance under CC-1 is stable after a few generations of crossing. The performance ratio (R_1) under CC-1 and RHMC after a few generations of crossing approximates:

$$R_{1\left(\frac{\text{CC-1}}{\text{RHMC}}\right)} = \frac{2(1 + 2H/3 + D/(3(2-D)))}{2+H}.$$

For D=0.1 and H=0.3, R_1 is 1.06; i.e. performance under CC-1 exceeds performance under RHMC by 6%.

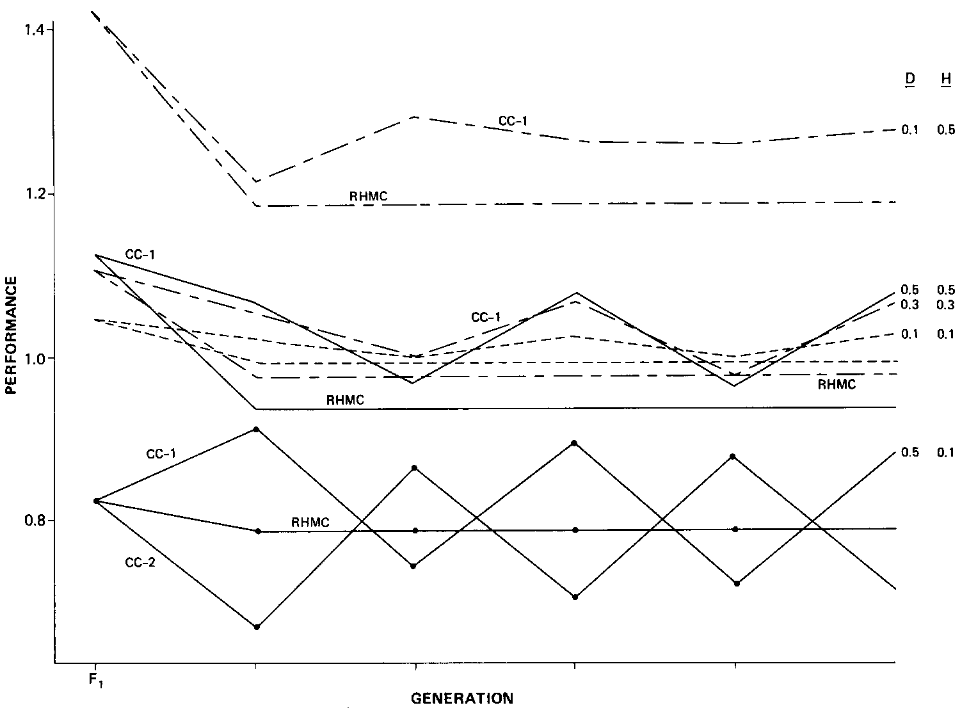

Fig. 1. Expected performance under crisscross (CC) and repeated hybrid male cross (RHMC) mating systems with relative performance 1 for the superior parent breed and 1-D for the other and heterosis H(2-D)/2. A) RHMC, CC-1 and CC-2 for D=0.5, H=0.1; B) RHMC vs CC-1 for D, H combinations 0.1, 0.1; 0.3, 0.3; 0.5, 0.5; C) RHMC vs CC-1 for D=0.1, H=0.5

Table 2. Expected performance under crisscross (CC · 1)[a] and the ratio of the performance under CC · 1 to the performance under repeated hybrid male cross (RHMC)

Generation	CC · 1	CC · 1/RHMC	CC · 1	CC · 1/RHMC	CC · 1	CC · 1/RHMC
	D=0.1, H=0.1[b]		D=0.2, H=0.1		D=0.3, H=0.1	
1 (F_1)	1.045	1.000	0.990	1.000	0.935	1.000
2	1.023	1.025	0.995	1.053	0.968	1.083
3	1.009	1.011	0.943	0.998	0.876	0.981
4	1.028	1.030	0.994	1.052	0.959	1.074
5	0.999	1.001	0.931	0.985	0.861	0.964
6	1.029	1.031	0.993	1.051	0.957	1.072
	D=0.1, H=0.2		*D=0.2, H=0.2*		*D=0.3, H=0.2*	
1 (F_1)	1.140	1.000	1.080	1.000	1.020	1.000
2	1.070	1.023	1.040	1.051	1.010	1.080
3	1.081	1.034	1.010	1.020	0.940	1.005
4	1.088	1.041	1.050	1.061	1.012	1.082
5	1.065	1.019	0.992	1.002	0.920	0.984
6	1.092	1.044	1.052	1.063	1.013	1.083
	D=0.1, H=0.3		*D=0.2, H=0.3*		*D=0.3, H=0.3*	
1 (F_1)	1.235	1.000	1.170	1.000	1.105	1.000
2	1.118	1.023	1.085	1.048	1.053	1.078
3	1.151	1.053	1.078	1.042	1.004	1.027
4	1.147	1.049	1.106	1.069	1.066	1.090
5	1.130	1.034	1.054	1.018	0.978	1.000
6	1.154	1.056	1.111	1.073	1.069	1.093

[a] Crisscross mating where males from a superior breed are used to mate with F_1 hybrid females
[b] Performance of two breeds is expressed as 1 and 1-D. H = heterosis. For details see the text

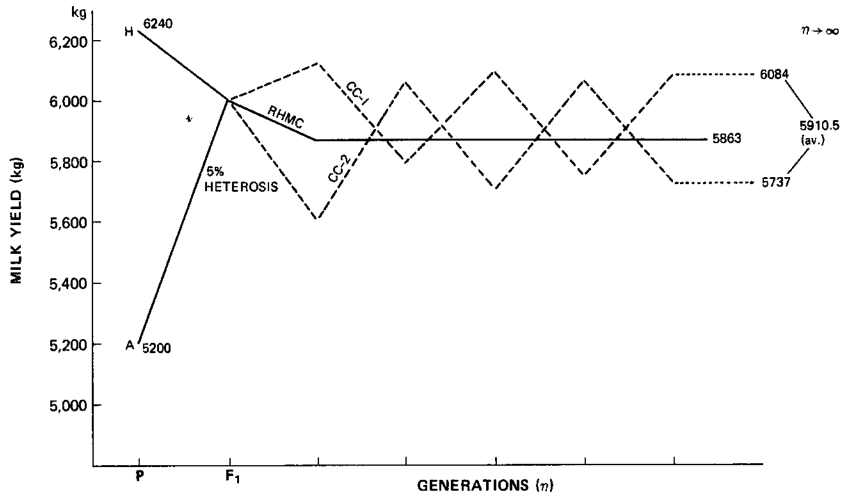

Fig. 2. Expected milk yield under crisscross (CC-1 and CC-2) and repeated hybrid male cross (RHMC). 1 and 2 for CC represent two breeds used for crossing

After a few generations of crossing, the ratio (R_2) of the averaged performance of two alternative CCs to the performance under RHMC approximates:

$$R_2\left(\frac{CC}{RHMC}\right)=\frac{6+4H}{6+3H}.$$

For R_2, the performance difference (D) is not involved, and CC is always superior whenever heterosis (H) is positive. The ratio R_2 is close to 1.0 when H is small, e.g., $R_2 = 1.008$ when heterosis (H) is 5% and $R_2 = 1.016$ when H is 10%.

A theoretical comparison for milk yield per lactation in dairy cattle assuming heterosis is 5% is shown in Fig. 2 assuming the parent breeds are Holsteins (H) and Ayrshires (A) with breed means respectively of 6240 and 5200 kg. Under the RHMC system milk yield is expected to be 5863 kg constantly after the F_1 generation while under the CC, milk yield is expected to zig-zag over generations, approaching a milk of 5910.5 kg averaged over CC-1 and CC-2.

Discussion

Heterosis in two-breed crosses of *Bos taurus* dairy cattle has been evaluated for several traits. The range of heterosis estimates from such studies is given in Table 3 for various yield, survival and reproduction traits. There is evidence of heterosis in the desired direction for all traits even though it is generally less than 10%.

The performance of dairy crossbreds from either the CC or RHMC systems for any of the single traits listed in Table 3 is not expected to exceed that of the superior parent line when heterosis is low even if parent line differences are small. However, cumulative or lifetime (length of herd life) performance in dairy cattle is a complex character in which the many component traits are expected to act multiplicatively rather than additively.

Conceptually, lifetime milk production, the primary determiner of lifetime profit, consists of average milk yield per lactation (M) and number of lactations during herd life (N). With heterosis H_M and H_N respectively, lifetime milk yield in crosses between two breeds is expected to be $\bar{M}\bar{N}$ $(1+H_M+H_N+H_M H_N)$ where $\bar{M}$ and $\bar{N}$ are breed averages for milk yield and number of lactations during herdlife, respectively. If for example, $\bar{M}=(M_1+M_2)/2=(6240+5200)/2$ kg, $\bar{N}=(N_1+N_2)/2=(3.2+5.1)/2$, $H_M=0.06$ and $H_N=0.12$, then the ratio of two-breed cross to parental mean for lifetime milk yield is 1.19. This example indicates that moderate heterosis (19%) in lifetime milk yield can be expected from less heterosis in component traits (6 and 12%). Heterosis of 20% or greater as assumed in the present study may be realistic for a complex trait such as lifetime performance, and has been demonstrated with mice (Nagai et al. 1980).

An economic evaluation of lifetime performance in dairy cattle requires quantification of both the expense and income aspects. Lifetime milk production primarily determines income while feed costs are the major expense. Survival rate, calving interval, reproductive rate, and disease resistance may also be involved in either or both income and expenses. Touchberry (1970) found from his comprehensive study by combining viability, growth and production into a measure of total performance expressed in terms of dollars that crossbreeding resulted in 21.7% heterosis. Results in table 2 would indicate an advantage for either the CC or RHMC systems over the superior parent breed in lifetime performance

Table 3. Percentage heterosis reported for several dairy traits in two breed crosses of *Bos taurus* dairy breeds

Trait	References	Heterosis (range) percent
Milk yield	Hollon et al. 1969 McDowell et al. 1974 Pearson and McDowell 1968	2.0 ~ 8.2
Milk fat yield	Hollon et al. 1969 Pearson and McDowell 1968	0.0 ~ 12.0
Days open	McDowell and McDaniel 1968a McDowell et al. 1970 McDowell et al. 1974	3.7 ~ 15.0
Days from calving to first estrus	McDowell et al. 1970 McDowell et al. 1974	−4.1 ~ − 2.9
Days from first breeding to conception	McDowell et al. 1970 McDowell et al. 1974	6.2 ~ 9.3
Percent pregnant by 90 (or 95), 120 and 145 days post partum	McDowell et al. 1970 McDowell et al. 1974	−0.7 ~ 11.5 7.3 ~ 13.9 −0.2 ~ 7.3
Calving interval	McDowell et al. 1974	1.0
Losses of females born alive, prior to first calving	McDowell and McDaniel 1968b	−3.0
Viability from 150 days gestation of the dam through first lactation of the offspring	McDowell and McDaniel 1968b	1.0
Services per conception	McDowell et al. 1974	−0.9
Veterinary cost	McDowell and McDaniel 1968c	−3.6

First lactation wherever relevant

for this level of heterosis and parent breed differences of less than 20%.

Evaluation of lifetime performance is an important element of both the crossbreeding and within-population selection aspects of a large dairy cattle breeding project in Canada (McAllister et al. 1980). Measurements of traits involved in lifetime performance which are being recorded include growth and body size and scale through to maturity, lactation milk and component (butterfat, protein and lactose) yields, lifetime reproductive performance including all heats and services, lifetime medical care records, calving ease and placental condition at each parturition, individual feed consumption and utilization in heifers and first lactation cows and detailed reasons for disposal. These measurements will be used to assess total economic merit of crossbreds in lifetime performance under the RHMC. In addition, the first generation of both CC-1 and CC-2 (i.e., backcrosses of the F_1 females to both parent line males) females are being produced and will be evaluated with the purelines and F_1's to assess heterosis, recombination loss and additive differences.

The discussion of the expected performance under CC and RHMC was based on the assumption that heterosis is realized as expected after the F_1 generation. Sheridan (1980) has questioned, after examining data from the literature, whether the present heterosis theory for breed crosses is valid to predict performance of crosses after the F_1 generation. He considers that epistatic interactions among dominant genes located at different loci may play a more important role in determining heterosis, than previously thought. McGloughlin (1980) demonstrated in a mouse experiment that a significant positive linear relationship exists between heterozygosity and heterosis, substantiating dominance as the primary determiner of heterosis. Further studies on heterosis are necessary to predict performance of dairy cattle under various mating systems such as CC and RHMC.

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Dr. J. Nagai
Dr. A. J. McAllister
Genetics Bldg. (No. 34)
Animal Research Centre
Agriculture Canada
Ottawa, Ontario K1A 0C6 (Canada)