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GENETICS AND BREEDING

Genetic Relationships and Linear Model Comparisons Between United States and Canadian Ayrshire and Jersey Bull Populations

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ABSTRACT

The ties and relationships within the Ayrshire and Jersey bull populations from the United States and Canada were investigated. Twenty-two percent of genes in the United States Ayrshire bull population were of Canadian origin, whereas 22% of genes in the Canadian Jersey bull population were of United States origin. Average genetic relationships among bulls between countries were comparable with the within country relationships. The BLUP animal model bull proofs for milk and fat production from each bull's country of evaluation were subsequently used to rank bulls across countries with a linear model. Genetic differences, differences in reference bases, and relative genetic progress in the various bull populations were also estimated. On the average in the last 20 yr the United States and Canada have produced and evaluated Ayrshire bulls of equal genetic merit for milk and fat, but the United States has produced and evaluated better Jersey bulls than Canada by .7 SD of milk and .6 SD of fat. The rate of genetic progress for either trait over that time, however, was similar in both countries and both breeds and ranged from .07 to .09 SD/yr. Across country proofs by the linear model were highly correlated with domestic animal model proofs and converted foreign proofs.

(Key words: genetic relationship, international comparison, bull populations)

Abbreviation key: AYR = Ayrshire breed, CAN = Canada, CONV = converted proofs,

ETA = estimated transmitting ability, GBR = Great Britain, ILJ = Isle of Jersey, JER = Jersey breed, MGS = maternal grandsire, NAP = North American proofs, PRF = animal model bull proofs.

INTRODUCTION

Semen and livestock have been extensively exchanged between the US and Canada (CAN) for most dairy cattle breeds. Breeders who import foreign germplasm, however, are unaware of the existence or the magnitude of genetic differences between the two populations, making it difficult to rank imported bulls in relation to locally proven bulls before the imported bulls receive an official evaluation in the importing country. Currently, proofs from the exporting country are converted to figures that compare with proofs in the importing country using regression techniques (5, 7, 8). The intercept of the regression attempts to account for differences in reference bases, and the slope accounts for differences in units of measurement. Techniques have been developed in this area that result in unbiased estimates of the coefficients (3, 11).

An alternative to within country conversions is to combine information from different countries and obtain an international BLUP estimate of each bull's transmitting ability (ETA) using a linear model. This approach makes use of bulls' ETA in each country and genetic relationships among bulls. Therefore, considerations of relationships between different bull populations are required for this approach.

Linear model methodology for across country bull comparisons was suggested by Schaeffer (10) and implemented by Rozzi (9) to compare Holstein-Friesian bulls from the US, CAN, and Italy and by Jacques and Klemetsdal (6) for Scandinavian dairy bull comparisons. In both cases, bull proofs by various sire models

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within country were used. Animal model proofs, however, better account for nonrandom mating of bulls than sire model proofs. Implementation of animal models also improved the genetic correlation between proofs from the US and CAN because all lactations were considered compared with only first lactations previously used in CAN.

The objectives of this study were 1) to investigate the ties and genetic relationships between bull populations from the US and Canada for both Ayrshire (AYR) and Jersey (JER), 2) to rank bulls for milk and fat production across countries and estimate the genetic differences between countries for each breed and trait, and 3) to compare linear model international proofs with converted foreign proofs.

MATERIALS AND METHODS

Genetic Relationships and Ties

Pedigree records including sire, dam, and maternal grandsire (MGS) of the bull were collected on the following bulls: 1873 AYR bulls registered in the US, 7759 AYR bulls registered in CAN, 133 AYR bulls registered in both countries, and 81 AYR bulls registered in Great Britain (GBR) but evaluated in either the US or CAN; records were collected similarly on 8370 JER bulls registered in the US, 4812 JER bulls registered in CAN, 54 JER bulls registered in both countries, and 18 JER bulls registered in the Isle of Jersey (ILJ) but evaluated in either the US or CAN. The national origin of each bull was determined by the national origin of his ancestors. For ancestors without pedigree, national origin was assigned by registration number. If a bull had any pedigree information at all, it was used according to the following model:

$$\text{Bull origin} = 1/2 \text{ sire origin} + 1/4 \text{ dam origin} + 1/4 \text{ MGS origin.} \quad [1]$$

The contribution of the dam actually reflects the contribution of the maternal granddam, assuming that both have the same origin. The model was applied separately for each breed. National origins were assigned by a recursive procedure, and four rounds of iteration were required until no further reassignments were

made. National origins represented probabilities that genes were from various populations. The national origin of each bull consisted of partial contributions from as many as three populations: US, CAN, and GBR in AYR and US, CAN, and ILJ in JER. The sum of the coefficients pertaining to each population for each bull was unity.

Genetic relationships between and within countries were estimated by the additive relationships among bulls and the national origin of each bull. Only relationships due to common sires and MGS were considered. Pairs of potential relationships included sire and son, MGS and grandson, paternal half-sibs, paternal half-cousins, maternal half-cousins, paternal grandsire and grandson, great grandsire and great grandson, and half-uncle and nephew. A procedure was developed to decompose the average additive genetic relationship among all bulls from both countries into within and between country components. Each relationship was decomposed according to a second-degree polynomial with elements representing probabilities that genes of the sire causing the relationship were from various populations. If these probabilities are p_i , for $i = 1, n$, for n populations of origin, and the additive genetic relationship is r , then the probability (pw) that a pair of genes are identical by descent and both come from the same population, i , is $(r)(p_i)^2$. Similarly, the probability (pb) that a pair of genes are identical by descent and come from two different populations, i and j , is $2(r)(p_i)(p_j)$. This procedure was applied to all bulls across the US and CAN, separately for each breed, and the average relationships were estimated similarly to Banos and Cady (1). All pw values contributed to average relationships within corresponding populations, whereas pb values contributed to average relationships between pairs of populations. Average relationships were estimated over all bulls from both countries. Therefore, average relationships between the US and CAN estimate cross-border ties relative to relationships within the US and within CAN. These values represent the probability that any two bulls from a pool of US and CAN bulls are related and originate from two different populations compared with the probability that these bulls are related and originate from the same population. These averages are underestimates of the true average relationships because the

female side of the pedigree was partially ignored. The relative values of the average components were of major interest.

Across Country Comparisons

Animal model 1989 bull proofs (PRF) for milk and fat yield were obtained from USDA and Agriculture Canada. Bulls were required to have at least five effective daughters and valid year of birth recorded. These requirements left 1772 AYR bulls evaluated in the US, 2299 AYR bulls evaluated in CAN, 7910 JER bulls evaluated in the US, and 2067 JER bulls evaluated in CAN. Bulls were born between 1950 and 1984.

The PRF were deregressed within country and breed using the method described by Banos et al. (2). These deregressed forms were subsequently standardized within country of evaluation to account for differences in units among countries and analyzed across countries and within breed and trait by the following model (10):

$$Y = Xc + ZQg + Zs + e \quad [2]$$

where:

Y is a vector of standardized deregressed proofs from each country, described by Banos et al. (2);

c is the country of evaluation fixed effect;

g is a genetic group fixed effect;

s is the bull within group random effect,
 $\text{Var}(s) = A\sigma_s^2$ A the numerator relationship matrix;

e is the random residual $\text{Var}(e) = R\sigma_e^2$,
 R^{-1} a diagonal matrix with diagonals equal to the number of effective daughters of each bull in each country of evaluation;

X, Z are incidence matrices; and

Q is a matrix that assigns bulls to genetic groups.

Genetic groups were defined by the year of birth and the national origin of each bull as defined in model [1]. To accommodate this model, the Q matrix included elements other than 0 and 1. There were as many as three nonzero elements in each row of Q. Twenty-

one groups were formed involving seven 5-yr periods and three countries of origin.

Heritability was .29 for both breeds and traits to compromise between the slightly different heritabilities used in the US and CAN evaluations. The model assumes that evaluations in each country have accounted for the important fixed effects within each country. The model also assumed uncorrelated residuals within country of evaluation and ignored bull by country interactions. Because prediction error covariances are ignored, accuracies of across country PRF would be less than for an evaluation from combined lactation data, but results will still be unbiased (10).

Comparison with Converted Proofs

In order to compare international PRF obtained by the linear model with the within country converted foreign PRF, regression coefficients were calculated as follows: CAN to US based on dually proven bulls either used first in CAN or used simultaneously in both countries for the first time. There were 62 AYR and 55 JER bulls that qualified. An analogous criterion secured 39 AYR and 75 JER bulls for US to CAN conversions. In either case, bulls were born within the last 20 yr and had daughters with records in at least 15 herds in both countries. The requirements set by INTER-BULL (4) had to be relaxed to include more bulls. Wilink's regression approach was used (11).

RESULTS AND DISCUSSION

Genetic Relationships and Ties

Average genetic contributions of population of origin to bulls registered in each country, by breed, are in Table 1. The fact that 22% of the genes of AYR bulls registered in the US are of CAN origin indicates the important role that the CAN AYR breeding program plays in the US. This contribution, however, is asymmetric because only 9% of the genes of CAN registered bulls are of US origin. The situation is reversed in JER: the US genes substantially influenced CAN cattle, whereas the CAN genes constituted only 4% of genes of all US registered bulls.

The average additive genetic relationship among bulls across countries was decomposed

TABLE 1. Average gene contribution (percentage) of population of origin to country of registration by breed.

Breed	Population of origin ¹	Country of registration	
		US	CAN
Ayrshire	US	76	9
	CAN	22	88
	GBR	2	3
Jersey	US	93	22
	CAN	4	74
	ILJ	3	4

¹CAN = Canada; GBR = Great Britain; and ILJ = Isle of Jersey.

to within and between country components shown in Table 2. Although these relationships are underestimates, their relative values are important. Components involving GBR AYR and ILJ JER only refer to relationships with bulls imported from these populations to the US and CAN and their descendants thereafter, so they do not reflect relationships associated with the entire GBR AYR and ILJ JER bull populations. If there were no relationships between countries, the corresponding components would have been zero, and the relative values of the within country components would be proportional to the size of each population and the strength of relationships within population. For AYR, the average relationship between US and

CAN is almost half as much as the average relationship within US, accounting for 6.4% of the overall average relationship. For JER, the US by CAN component was 11.3% of the total average relationship and higher than the within CAN component, reflecting the influence of US genetics on CAN bulls. These observations are in agreement with results in Table 1 and indicate that extensive exchange of genetic material, although asymmetric, has resulted in the development of ties and relationships between the US and CAN populations for both breeds.

Across Country Comparisons

All solutions are expressed in standardized form and can be back-transformed to original within country units after being multiplied by the SD of the within country PRF. Because the base for age adjustment of records was specific to each country, conversion of these values to an international unit, for example kilograms, should be treated with caution.

North American proofs (NAP) were estimated as $Qg + s$. Difference between country solutions, c , was .078 for milk and .012 for fat in AYR and 1.207 for milk and 1.087 for fat in JER, in favor of the CAN evaluation system. These values reflect differences in reference bases of the two countries and do not estimate genetic differences between countries.

Average NAP by national origin and time of birth for AYR and JER are in Figures 1 and 2

TABLE 2. Average genetic relationship among all bulls, between and within populations components, and percentage of total each component accounts for, by breed.

Breed	Component ¹	Average relationship	Percentage
Ayrshire	All	.001797	100.0
	US by US	.000235	13.1
	CAN by CAN	.001395	77.6
	US by CAN	.000115	6.4
	US by GBR	.000008	.5
	CAN by GBR	.000025	1.3
	GBR by GBR	.000019	1.1
Jersey	All	.001324	100.0
	US by US	.000994	75.1
	CAN by CAN	.000127	9.6
	US by CAN	.000150	11.3
	US by ILJ	.000030	2.3
	CAN by ILJ	.000005	.4
	ILJ by ILJ	.000018	1.3

¹All = All bulls across countries; CAN = Canada; GBR = Great Britain; and ILJ = Isle of Jersey.

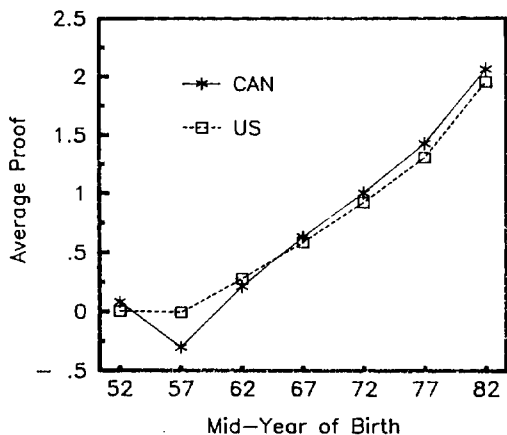


Figure 1. Average North American milk proofs of Ayrshire bulls in standard deviations by national origin and year of birth.

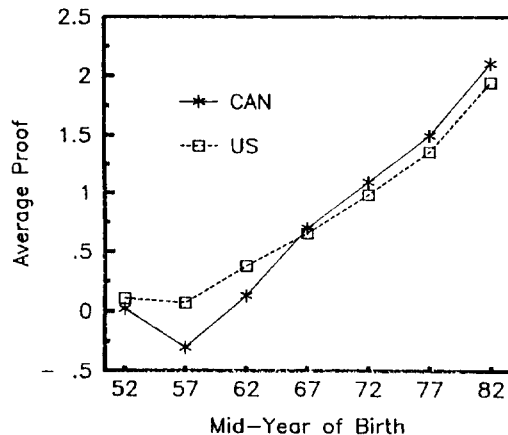


Figure 3. Average North American fat proofs of Ayrshire bulls in standard deviations by national origin and year of birth.

for milk and 3 and 4 for fat, respectively. Year of birth is the midyear in a 5-yr period. Here a bull's contribution to a population's average is determined by the proportion of this bull's genes coming from the particular population. These values illustrate genetic differences among bulls originating from different populations, irrespective of country of PRF. Linear trends in US and CAN were estimated for the last 20 yr and are shown in Table 3 by breed and trait. These values reflect genetic improvement of .07 to .09 SD/yr in the bull populations

of both countries and both breeds and traits. In the US, the average genetic gain was higher for milk than fat, showing the relative emphasis placed on volume by breeders of both breeds. In CAN, fat production seems to have been given emphasis equal to that on milk production in the breeding programs of AYR and JER. Over these 20 yr, AYR bulls originating in CAN were on the average .06 ($\pm .13$) SD better than bulls originating in the US for both milk and fat. These differences are not significant at the .05 level. At the same time, JER bulls

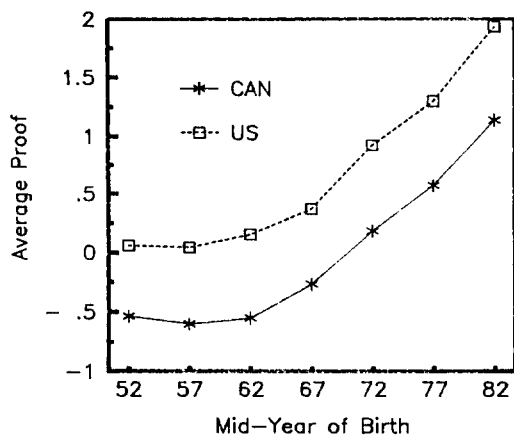


Figure 2. Average North American milk proofs of Jersey bulls in standard deviations by national origin and year of birth.

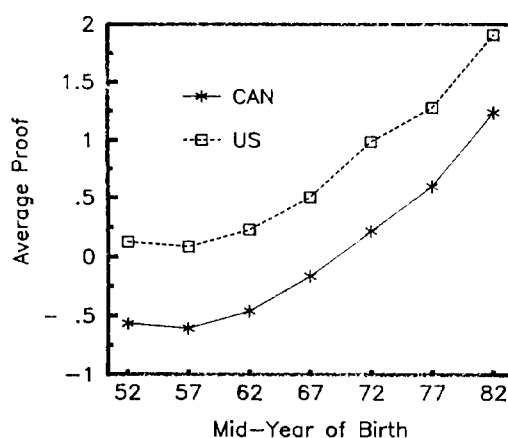


Figure 4. Average North American fat proofs of Jersey bulls in standard deviations by national origin and year of birth.

TABLE 3. Linear genetic trends in SD over 5-yr periods for bulls born between 1960 and 1984 by national origin, trait, and breed.

Breed	Country of origin ¹	Milk		Fat	
		Trend	SE	Trend	SE
Ayrshire	CAN	.40	.04	.37	.03
	CAN	.44	.03	.46	.03
Jersey	US	.45	.04	.41	.03
	CAN	.40	.03	.40	.03

¹CAN = Canada.

²Standard errors.

originating in the US were on the average .71 ($\pm .14$) SD higher than bulls originating in CAN for milk and .62 ($\pm .13$) SD higher for fat.

Similar genetic trends and genetic differences were observed over the last 20 yr when average NAP by country of evaluation and time of birth were considered. Average differences between AYR bulls evaluated in the US and CAN were not significantly different from zero for either trait, whereas the US evaluated JER bulls exceeded CAN evaluated bulls by .70 ($\pm .14$) SD for milk and .61 ($\pm .13$) for fat.

Within each country, NAP were expressed to the same base as for bulls in that country by adding the corresponding country solution and back-transforming to original units. Rank correlations between NAP-US and PRF-US, as well as between NAP-CAN and PRF-CAN, for all bulls evaluated in each country and for the top 100 by NAP, by breed and trait, are shown in Table 4. Changes in rankings occurred only for certain bulls, imported from the other country, that were evaluated with lower accuracy in the importing country than the country of origin.

Preferential mating should not cause reranking, assuming proper identification of dams within country; however, preferential treatment of progeny of sires with imported semen could be a factor in reranking. The international model removed some bias of preferential treatment on the PRF in the importing country by accounting for the country of origin of the bulls. The direction of the reranking was determined by the rank of the bull in the country of origin. Use of the international linear model effectively combined information from both countries to estimate NAP.

Changes in rankings were observed among the best bulls in each country because of the high merit of the imported bulls. Presence of imported bulls at the top of the rankings demonstrates the influence of one country's genetic material on the other as well as the effectiveness of the second country in selecting foreign bulls to import. This was the case with AYR CAN bulls in the US and JER US bulls in CAN.

Comparison with Converted Proofs

Conversion coefficients by direction of conversion, breed, and trait are shown in Table 5. The intercepts in each case estimate differences in reference bases. Because CAN bases move each year, these estimates pertain only to 1989 data. Differences in country solutions from the linear model, which also estimate reference base differences, are included in Table 5. Country solutions in each case were back-transformed to the original units and were then compared with the intercepts. Discrepancies between the estimates may occur because intercepts were estimated on a limited number of

TABLE 4. Rank correlations between North American proofs and animal model proofs including all bulls (RALL) and only the top 100 by NAP (R100) by country of proof, trait, and breed.

Breed	Country of proof ¹	Number of bulls	Milk		Fat	
			RALL	R100	RALL	R100
Ayrshire	US	1772	.98	.78	.99	.85
	CAN	2299	.98	.94	.99	.95
Jersey	US	7910	.99	.98	.99	.98
	CAN	2067	.99	.79	.99	.87

¹CAN = Canada.

TABLE 5. Intercepts (INT) and slopes (SLP) of foreign proofs conversion formulas and corresponding differences in country solutions from the linear model back-transformed to original units (DC) by direction of conversion (DIR), breed, and trait.

Breed ¹	DIR ²	Number of bulls	Milk			Fat		
			INT	SLP	DC	INT	SLP	DC
AYR	US to CAN ³	39	.78	.01	.62	.91	.28	.10
	CAN to U'S ⁴	62	-132.89	86.42	-41.51	-3.19	3.42	-.23
JER	US to CAN ³	75	10.45	.02	9.83	7.83	.29	7.62
	CAN to US ⁴	55	-947.75	80.24	-779.45	-34.13	3.61	-27.30

¹AYR = Ayrshire and JER = Jersey.

²CAN = Canada.

³Values are in Canadian mature equivalent Breed Class Averages.

⁴Values are in United States mature equivalent pounds.

bulls. Absolute values of the intercepts were greater than country solution differences, indicating that intercepts may also contain some genetic differences between populations that accumulate over time. These genetic differences are expressed as genetic group differences in the linear model.

Two alternative systems for across country ranking of bulls were considered: by NAP and by a combination of PRF and converted PRF (CONV) of bulls from the other country. Rank correlations between the two lists for all bulls and for the top 100 bulls by NAP by country of PRF and breed are given in Table 6. Within country rank correlations between NAP and CONV of bulls from the other country not evaluated in the country of consideration are also given in Table 6. In both countries and both breeds, the rank correlation between NAP and CONV was almost perfect, indicating that

both methods may result in similar ranking of bulls in the other country when only two countries are involved. Rank correlations between NAP and the PRF-CONV combination over all bulls were .97 or better in both breeds and traits. Lowest values were observed for fat in AYR, for which the discrepancy between the regression intercept and the country solution difference was largest. Reranking in the list of the best 100 bulls by NAP was less severe than among bulls evaluated in each country (Table 4) and was observed only for NAP-US with PRF-US and CONV-US. Reranking was again due to some imported bulls evaluated with less accuracy in the importing country than in their country of origin. However, rank correlations of NAP with PRF and CONV for the best 100 bulls by NAP across countries were higher than rank correlations between NAP and PRF for the best 100 bulls by NAP within country (e.g., US

TABLE 6. Rank correlations of North American proofs with animal model domestic proofs and converted foreign proofs, including all bulls across countries (RALL) and only the top 100 by NAP (R100), and rank correlations between NAP and converted proofs of foreign bulls (RCONV), by country of proof, breed, and trait.

Breed ¹	Country of proof ²	Number of bulls	Milk		Fat		Number of bulls	RCONV	
			RALL	R100	RALL	R100		Milk	Fat
AYR	US	3969	.98	.83	.97	.85	2197	.99	.99
	CAN	3969	.98	.94	.97	.95	1670	.99	.99
JER	US	9835	.99	.98	.99	.98	1925	.99	.99
	CAN	9835	.99	.98	.99	.95	7768	.99	.99

¹AYR = Ayrshire and JER = Jersey.

²CAN = Canada.

AYR or CAN JER). This was due to the presence of superior bulls from the other country (e.g., CAN AYR or US JER, respectively) that were not evaluated in the country of consideration and whose CONV were highly correlated with their NAP.

CONCLUSIONS

Genetic ties and relationships have been developed between the US and CAN in the AYR and JER breeds. Ayrshire CAN genes make up almost one quarter of all genes in the US breeding bull population, whereas JER US bulls contribute almost one quarter of the genes to the corresponding CAN populations. As a result, in AYR the average genetic relationship between the US and CAN is as high as half the average relationship among bulls within the US; in JER, the average genetic relationship between countries is even higher than the average genetic relationship within CAN.

Existence of ties and genetic relationships between the US and CAN make possible the simultaneous comparison of bulls across countries with a linear model and the estimation of genetic differences between the bull populations in these countries. Such comparisons suggest that since 1960 US and CAN AYR remained competitive with each other in terms of bulls produced and evaluated for milk and fat production. Canada has produced slightly better bulls on the average, but the US has been efficiently using superior bulls from both sides of the border. In JER, US has produced and evaluated bulls superior to CAN by about .7 SD for milk and .6 for fat, but the rate of genetic improvement among bulls has been almost the same in both countries for the last 20 yr, amounting to .07 to .09 SD/yr.

The linear model effectively combined information from both countries, accounting for the number of daughters each PRF was based on and emphasizing the population of origin, to rank bulls on a common basis. This NAP ranking is of interest to breeders and producers in the US and CAN because it can help them identify superior bulls from each other's population and directly compare them with its own. Furthermore, ranking of bulls by NAP would interest the dairy industry in countries that consider importing North American genetics.

The system can be expanded to include more

than two countries and traits, provided that each participating country implements an animal model for its own evaluation to account for nonrandom mating of imported bulls. This model should also account for similar fixed effects in each country for each trait. A common age for record adjustment prior to evaluation should be adopted by participating countries.

In this study CONV based on foreign bulls and NAP were highly correlated although the former were estimated from regressions based on relatively small numbers of highly selected bulls. Implementation of the animal model might have removed certain biases in PRF that were affecting conversions in the past. If, however, more than two countries are considered, across country ranking of bulls with a linear model may be more interesting than pairwise conversions because it would combine progeny information on each bull from different countries and would provide simultaneous comparisons of bulls on an international basis. Such rankings would facilitate selection decisions of perspective importers as well as sire analysts.

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