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Genetic Relationship Between the United States and Canadian Holstein Bull Populations¹

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ABSTRACT

The average additive genetic relationship and degree of connectedness between American and Canadian Holstein AI bull populations were estimated. This project was undertaken to determine the feasibility of a joint United States-Canadian sire evaluation to estimate genetic base differences between the two countries' Holstein bull populations. Data were provided by USDA and Agriculture Canada for bulls evaluated in each country. Bulls were designated as American, Canadian, or dual national origin based on their country of registration and national origin of their parents. A total of 13,079 American, 1683 Canadian, and 256 dual origin bulls were included in the inverse relationship matrix. When both sire and maternal grandsire relationships were included in the matrix, there were 174 disconnected groups; however, 99% of the American bulls and 97% of the Canadian bulls were in a single group. The average a_{ij} between the American and Canadian population was 4.6×10^{-5} . Despite the low average additive relationship between the two national populations, the high degree of connectedness in the inverse relationship matrix, when using both sire and maternal grandsire relationships, suggests sufficient genetic ties between the two populations to conduct a meaningful joint sire evaluation.

INTRODUCTION

The United States and Canada are among the countries leading in export of dairy cattle germ plasm. Countries that import germ plasm to incorporate foreign genetic material into their indigenous breeding programs do not know the average difference in genetic merit for economically important traits between populations (7). Extensive sale of bull semen to foreign markets, as well as exchange between the United States and Canada, necessitates knowing the difference between the genetic bases of the two countries. To date, no direct comparison between all bulls of distinct national populations has been made.

Some attempts have been made to compare bulls from Canadian and US populations (5, 8, 9) and to compare several populations of bulls simultaneously (10). In addition, several attempts have been made in the European community to standardize methods for bull proving and determine base differences in European dairy cattle populations (7). Two of the studies (5, 8) included only bulls that had evaluations in both the US and Canada, which limited the population size and had the potential of introducing bias into the evaluation due to the selected use of imported semen in both countries. Other studies (9, 10) examined a relatively small number of bulls in relation to population sizes and therefore the genetic values of the sample of bulls used may not have been indicative of differences between the two populations.

One possible solution to the problem of estimating genetic base differences between populations of individual countries would be a simultaneous BLUP evaluation of all bulls used in AI in each population in question using lactation records from daughters regardless of the country in which they are made (12). Successful completion of such an evaluation requires sufficient ties (connectedness) in the

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mixed model equations (MME) between bulls from populations in question in order that national populations not be evaluated as independent groups (11). Connected elements of a matrix are elements that share the same row or column (11). One source of ties is provided through bulls being used in common herd-year-seasons (HYS). Another source is available when the inverse relationship matrix (A^{-1}) is included in a BLUP evaluation, which not only reduces bias due to selection (2, 3) but increases connectedness in the MME through genetic ties.

Bulls i and j are tied together genetically when a_{ij} in the A^{-1} is nonzero. Genetic ties are not necessarily limited to individuals of common ancestry as a genetic tie may also exist between individuals with common descendants. For example, a bull's sire and maternal grand-sire (MGS) may be unrelated (without common ancestors), but the sire and MGS are genetically tied through their common relationship to the bull.

Geographically separated populations are not likely to have many HYS ties between them (be well-connected through HYS), relative to the size of the populations, unless there is equal access to germ plasm from each population (13). Because Canadian and American dairy cattle breeders do not have equal access to germ plasm from both countries, successful estimation of base differences between these populations, using only field data from each population, would be dependent on genetic ties between bulls as defined by the degree of connectedness of their associated elements in A^{-1} .

Exchange of semen and cattle between the US and Canada has established some genetic ties or relationships between the Holstein dairy populations in the two countries. This study was undertaken to examine the extent of the genetic relationship and connectedness in A^{-1} between AI bulls from the US and Canadian Holstein populations to determine the feasibility of a joint evaluation for the purpose of establishing the difference in the genetic bases of the two countries.

MATERIALS AND METHODS

Data were provided by USDA, ARS, and Agriculture Canada (Ag Canada). Sire summary information from USDA's July 1983 sire

evaluation was sent on a 380 format tape; Ag Canada sent a similar tape containing information from the January 1984 sire evaluation. The USDA also provided a tape crossreferencing registration numbers for 5017 bulls known to be registered in both countries' Holstein Registries.

The files were edited to eliminate all non-AI and all nonregistered Holstein bulls. Only AI bulls were considered in the study because: 1) primary consideration for semen export in the world market is given to AI proven bulls, 2) only AI bulls are genetically evaluated in Canada, and 3) the majority of the current cow populations in both Canada and the US are descendants of AI bulls.

Further editing eliminated bulls that lacked a valid date of birth. Records that lacked or had invalid sire, MGS, or dam identification were kept as long as there was a valid registration number and birth date for the bull. The resultant US file contained pedigree information on 12,499 bulls while the Canadian file contained information on 2631 bulls. Bull records in both files were checked against the crossreference tape, and any bulls that were registered in both countries had their record augmented with the second registration number. The two files were merged and duplicate records removed. The resultant file contained 14,675 bulls. Each record contained the bull's registration number, his sire's, dam's and MGS's registration number if known, the bull's birth date, the second country's registration number if known to exist, and for bulls evaluated by USDA, the number of daughters' records used in the USDA evaluation for that bull.

Defining bulls as American or Canadian was necessary to designate national groups for evaluation. Nationality of a bull was assigned according to the nation of registration and national origin of the bull's ancestors; therefore, the nationality of a bull's ancestors had to be determined first. This was done primarily on the basis of the number of digits and value of the registration number of the ancestor; Canadian numbers generally were smaller than the American numbers. Some difficulty was encountered in assigning nationality to dams of the oldest US bulls because of overlap in the registration numbers of the two countries. These ambiguous situations were resolved by assigning the same nationality to the dam as

that assigned to her sire as determined by his registration number.

All possible assignments of bulls to each nationality are summarized in Table 1. The expected norm was that a bull registered in only one country would be from parents of the same nationality. Another expected situation was that there would be bulls registered in a particular country born of a dam from the same country but a sire of the other nationality, for example, a bull with a Canadian registration number born to a Canadian cow by an American sire. In these situations, nationality of the bull was assigned as the country of registration for the bull and nationality of his dam. In the example cited, the bull was assumed to be the result of a Canadian breeding program and, therefore, of Canadian origin, despite the use of an American sire. The "dual" category was introduced to cover cases where country of origin was not always clear, such as if a bull with an American registration number was born to a Canadian cow and an American bull. In this case, the identity of the breeding program was ambiguous.

The bull file was sorted in ascending sequential order by registration number of the bull; therefore, many bulls appeared later in the file as sires or MGS to other bulls. Because a bull's nationality may have been reassigned and not updated later in the file, a recursive procedure was used to assign nationalities. Four rounds of

the procedure were required before no more reassignments were made. The data file was then augmented to include nationalities of the bull, sire, dam, and MGS. A list of bulls, known as the base population, which appeared in the file as sires and MGS's but without any tested daughters was prepared. These bulls, which had no known ancestors, were assumed to be non-inbred and were added to the beginning of the pedigree file. This increased the file size to a total of 15,018 bulls.

Two approaches were used to build A^{-1} . Both resulted in the creation of an A^{-1} following Henderson's method (4). One approach was to create A^{-1} utilizing only the bulls' sire relationships and will be referred to as the sire-only design. The second method utilized sire and MGS's relationships in order to take advantage of an expected increase in the average number of ties per bull. This method will be referred to as the sire-MGS design.

All female relationships were ignored in the various A^{-1} in order to reduce A^{-1} to a manageable size. This indicates that an assumption was made that there were no full-sib or maternal half-sib relationships among bulls evaluated. There is precedent for this assumption as set by the USDA Modified Contemporary Comparison (MCC), Northeast Artificial Insemination Sire Comparison, and the Canadian sire summary evaluations (1, 4, 6).

The two A^{-1} matrices produced were

TABLE 1. Conditions used to determine a bull's nationality and the number of bulls in each category.

Dam's nationality	Sire's nationality		
	US	Canadian	Dual
	Bulls registered in the US		
US	US/11,702	US/503	US/24
Canadian	Dual/13	Canadian/2	Canadian/1
Dual	US/0	Dual/0	Dual/0
	Bulls registered in Canada		
US	US/443	Dual/177	US/7
Canadian	Canadian/327	Canadian/1196	Canadian/41
Dual	Dual/7	Canadian/14	Dual/1
	Bulls registered in both US and Canada		
US	US/121	Dual/40	Dual/2
Canadian	Dual/16	Canadian/38	Dual/0
Dual	Dual/0	Dual/0	Dual/0

examined for the degree and nature of the connectedness between bulls. Connected elements of each A^{-1} matrix were collected into a submatrix (connected group) distinct from other connected element groups within the A^{-1} . Bulls represented in each submatrix were tied together via the connected elements, and there were no ties between bulls of distinct submatrices and no bull appeared in more than one submatrix. The number of nonzero elements in the two A^{-1} was also examined.

Average additive relationships between and within the various populations were estimated. Only sire-son, MGS-grandson, paternal half-sib, paternal half-sib/maternal half-cousin, and maternal half-cousin relationships were considered. The a_{ij} values for the identifiable relationships are shown in Table 2. All the described pairwise combinations of bulls were identified and assigned an a_{ij} value and used to build A .

The A (and A^{-1}) matrix can be partitioned as follows:

$$A = \begin{bmatrix} A_U & A_{UC} & A_{UD} \\ A_{CU} & A_C & A_{CD} \\ A_{DU} & A_{DC} & A_D \end{bmatrix}$$

Where $A_U = A$ for US bulls, $A_C = A$ for Canadian bulls, $A_D = A$ for dual nationality bulls, $A_{UC} =$ submatrix of a_{ij} between US and Canadian bulls, $A_{UD} =$ submatrix of a_{ij} between US and dual nationality bulls, and $A_{CD} =$ submatrix of a_{ij} between Canadian and dual nationality bulls. The mean a_{ij} for A_U , A_C , and A_D for $i \neq j$ is:

$$1/(n^2 - n) \sum_{i=1}^n \sum_{\substack{j=1 \\ i \neq j}}^n a_{ij} \quad [1]$$

Where $A_X = A_U$, A_C , or A_D and $n =$ the order of A_X . The mean a_{ij} for A_{UC} , A_{UD} , and A_{CD} is:

$$1/rc \sum_{i=1}^r \sum_{j=1}^c a_{ij} \quad [2]$$

Where $r =$ the number of rows in A_{XY} and $c =$ the number of columns. The resulting means are known to be underestimations of

TABLE 2. Summary of identifiable relationships between bulls when ignoring female relationships.

Relationship	Additive value
Sire-son	.5
Maternal grandsire-grandson	.25
Paternal half-sib/half-cousin	.3125
Paternal half-sib	.25
Maternal half-cousin	.0625

the true average a_{ij} , since full-sib, maternal half-sib, paternal half-cousin, and other more complex relationships were not included in the calculations.

RESULTS AND DISCUSSION

Table 1 is a summary of how many bulls were assigned to each nationality. As expected, most bulls of a particular country of registration had parents of the same nationality. The table does not include 279 American bulls and 64 Canadian bulls that were identified as base population bulls and were added to the list of bulls. The total number of American bulls in the final file was 13,079. There were 1683 Canadian bulls and 256 dual nationality bulls.

A high degree of disconnectedness existed among bulls when using the sire-only method of determining A^{-1} . The bulls segregated into 765 distinct disconnected groups. Three of the groups had more than 1000 members, 5 groups had between 500 and 1000 members, and 12 groups had between 100 and 500 bulls in the group. There were 367 bulls that belonged to single member groups, meaning they had no known relatives. Despite the large number of disconnected groups, over 50% of the bulls belonged to one of the 6 largest groups, and 90% belonged to one of the largest 56 groups, each of which had at least 15 members.

Composition and size of the 6 largest groups for the sire-only method are summarized in Table 3. The three largest groups together (#565, #251, #400) contained 5890 bulls; 5763 were of US origin. If bulls were distributed randomly among disconnected groups, the expected percentage of American bulls in any one group would be 87%. Therefore, the three largest groups appear to contain a disproportionate number of American bulls

(97.8%). The groups summarized are indicative of the situation in the 56 largest groups in that the distribution of bulls within a group appeared to be nonrandom, and groups could usually be classified as either predominantly American or predominantly Canadian. Chi-square tests of the distribution of sires by nationality within the largest 56 groups were significant at $P < .05$ for 39 groups. The fact that groups are somewhat multinational indicates that nonnative bulls have been used as sires of bulls in both countries; however, the nonrandom distribution of bulls within groups suggests that there has been limited and selected use of nonnative bulls in each country.

A joint evaluation based on the sire-only method of computing the A^{-1} would depend heavily on HYS ties to augment the apparent weak genetic ties that exist between the American and Canadian groups when using the sire-only method to compute A^{-1} . The source for the HYS ties would be daughters of Canadian bulls in US herds and daughters of American bulls in Canadian herds. However, as already stated, the source of HYS ties between the two populations is presumably not large relative to the size of the populations; therefore, it is questionable as to how useful a joint BLUP evaluation might be if only bulls' sires were used to calculate A^{-1} .

Using the sire-MGS method for computing A^{-1} , there were 174 disconnected groups; however, one group included 14,818 of the 15,018 bulls (98.7%). There was an average of 4.44 ties per bull in the group. Table 4 summarizes the size and composition of all groups. The single

largest group contained 98.9% of the American bulls, 96.9% of the Canadian bulls, and 98.8% of the dual nationality bulls. The existence of a single large genetic group that includes all but a very small number of bulls (no more than would be present in a distinct national population) is compelling evidence that sufficient genetic ties exist between the Canadian and American populations to conduct a valid evaluation for determining base differences. Herd-year-season ties would supplement the genetic ties in such an evaluation, but the evaluation would not be dependent on HYS ties.

Further investigation was done on the single large group to determine the number of bulls that provided the basis for the group. Table 5 lists the top 5 American bulls and top 5 Canadian bulls in number of ties to the group. The 20 Canadian bulls with the most number of ties each had a minimum of 73 ties. There were in excess of 45 American bulls with at least 75 ties each, bringing the total number of heavily tied bulls to 65; therefore, the matrix is not weakly connected by only a very few elite bulls.

Table 6 is a summary of the nature of cross-border ties between Canadian and American bulls. As expected, the number of bulls with cross-border ties increased from 1320 (8.8% of the total population) in the sire-only design to 2264 (15.1% of the population) in the sire-MGS design. The average number of cross-border ties over the entire population of bulls was 1.07 for the sire-MGS method and an average of 4.44 ties when ignoring nationality,

TABLE 3. Size, national composition, and chi-square statistic for the six largest distinct bull groups from the sire-only method.

Group no.	Number of bulls			χ^2
	US	Canadian	Dual	
565	2259	25	2	279.6**
251	1965	88	4	131.6**
400	1539	5	3	210.5**
20	271	443	84	2016.7**
39	396	164	72	503.2**
136	597	5	0	78.5**

** $P < .01$.

TABLE 4. Sire and national composition of each distinct bull group using the sire-maternal grandsire method.

Frequency of group size	Size of group	Number of bulls		
		US	Canadian	Dual
1	14,818	12,934	1631	253
1	6	6	0	0
1	5	5	0	0
3	2 @ 4	4	0	0
	4	0	4	0
1	3	3	0	0
7	2 @ 2	2	0	0
	4 @ 2	0	2	0
	2	1	1	0
160	118 @ 1	1	0	0
	39 @ 1	0	1	0
	3 @ 1	0	0	1

TABLE 5. The number and nationality distribution of ties and number of US daughters for the five American and five Canadian bulls with the most ties in the sire-maternal grandsire method.

Bull's registration no.	Number of ties to			Number of daughters ¹
	US	Canadian	Dual	
US bulls				
1491007	2271	77	25	52,513
1427381	1473	14	16	17,250
1450228	1180	22	4	29,230
1458744	1051	61	27	49,858
1556373	860	11	4	19,709
Canadian bulls				
308691	340	132	27	NA ²
275932	140	206	8	NA
267150/1492073 ³	67	219	25	NA
288790	86	146	15	NA
295768/1560362 ³	184	23	6	2364

¹ United States only.² Not available.³ First number is the Canadian registration number; second number is the US registration number.

which means the cross-border ties comprise over 25% of all ties in sire-MGS A^{-1} . Under both methods of computing the A^{-1} , there were fewer Canadian bulls with cross-border ties than American bulls, but the percentage of the Canadian bull population with ties to the American bull population is considerably higher than the converse relationship. Of those bulls with cross-border ties, Canadian bulls averaged about twice as many ties to American bulls as compared to American bulls with ties to Canadian bulls. This evidence supports the suggestion that American germ plasm plays a larger role in Canadian breeding programs than Canadian germ plasm plays in American programs. The effect of this disproportionate use of foreign semen by Canadian breeders is that there are relatively more sons of American bulls in Canada than sons of Canadian bulls in the United States. Consequently, Canadian bulls play a larger role in connecting the two national populations than might be expected, based on the size of the Canadian population relative to the American population. This in no way affects the general conclusion, however, that the two countries'

Holstein bull populations are sufficiently tied together to be evaluated jointly using the sire-MGS design.

A summary of the average additive relationships among the 15,018 bulls, and the percentage of nonzero elements in the A^{-1} off-diagonal elements are shown in Table 7. The within-nationality averages of a_{ij} (within American and within Canadian) are approximately the same ($P < .01$); however, the average additive relationship between American and Canadian bulls is small, and the standard error suggests it is not significantly different from zero. The inclusion of known female relationships in A^{-1} would increase the average a_{ij} and the existence of known ties between the two populations means that the average relationship must be greater than zero. The lower a_{ij} between populations than within populations provides further evidence that although nonnative bulls are used to supplement national breeding programs, they are not the major contributors to the national genetic breeding programs.

The percentage of nonzero off-diagonal elements is much higher in the within-nationality submatrices than in the between-nationality

TABLE 6. Number of bulls from one nationality group with ties to another nationality group and the average number of ties.

Ties	No. of bulls	Percentage of nationality with ties	Average ties	
			For bulls with ties	Over entire nationality
Sire-only design				
US to Canadian	559	4.2%	1.48	.06
US to dual	57	.4%	1.01	.004
Canadian to US	371	22.0%	2.23	.49
Canadian to dual	82	4.9%	3.06	.15
Dual to US	39	15.2%	1.59	.24
Dual to Canadian	212	82.8%	1.18	.98
Total	1320	8.8%	1.72	.47
Sire-MGS¹ design				
US to Canadian	1044	7.9%	1.78	.14
US to dual	158	1.2%	2.11	.03
Canadian to US	482	28.6%	3.85	1.10
Canadian to dual	122	7.3%	2.87	.21
Dual to US	225	87.9%	1.48	1.31
Dual to Canadian	233	91.0%	1.50	1.37
Total	2264	15.1%	2.24	1.07

¹ Maternal grandsire.

TABLE 7. Average additive relationship and percentage of nonzero elements within and between nationality groups.

Submatrix	Matrix order	Percentage of off-diagonal elements in A^{-1} not equal to 0		Average a_{ij}	
		Sire-only	Sire-MGS ¹		
SE					
Within					
US-US	13,079	.013%	.032%	.00495	.00006
Canadian-Canadian	1683	.081%	.202%	.00501	.00392
Dual-dual	256	.009%	.038%	.00013	.02170
Between					
US-Canadian	13,079 × 1683	.004%	.008%	.00005	.00093
US-dual	13,079 × 256	.002%	.009%	.00003	.01866
Canadian-dual	1683 × 256	.058%	.081%	.00383	.07739
Total	15,018	.013%	.029%	.00384	.00010

¹ Maternal grandsire.

submatrices, which supports the claim that the two national subpopulations are more related to themselves than they are to each other. However, the sire-MGS method increases the degree of filling in the between-national group submatrices to the same degree as in the within-national group submatrices of the sire-only method. This supports the conclusion that the number and nature of genetic ties between the US and Canadian Holstein AI bull population is sufficient to conduct a joint genetic evaluation, provided sire and MGS relationships are included in the A^{-1} .

CONCLUSIONS

Although nonnative bulls make up only a minor portion of either country's breeding program, comparing bulls in the two countries is of interest. A suggested method of determining the difference between the genetic bases would be to conduct a joint BLUP evaluation, provided sufficient genetic ties exist between the two populations. Because 98.7% of the bulls of the joint population belong to the same genetic group when the sire-MGS method is used to calculate A^{-1} , adequate genetic ties probably do exist. Further, for both countries many heavy use bulls, in terms of number of tested daughters and number of genetic ties, belong to the same group. The number of these heavy use

bulls is substantial and at least 65 bulls (45 American and 20 Canadian) contribute more than 70 ties each and 2264 (15.1% of the combined bull population) have cross-border ties. Furthermore, over 25% of all genetic ties are cross-border ties. Additionally, there is a high probability that daughters of the bulls in the groups will provide HYS ties. The relative percent of the Canadian bull population with cross-border ties compared with the American bull population suggests that the Canadian breeders use a larger percentage of US semen in their national breeding program than vice versa. Consequently, the Canadian bulls play a larger roll in tying the two populations together than might be expected based on the relative size of the national populations.

The sire-only method was examined to determine if the simplified calculations would provide sufficient genetic ties to do a simplified joint sire evaluation. Although possible, the sparser A^{-1} derived by the sire-only method forces the evaluation to rely heavily on HYS ties. Therefore, the sire-MGS method of calculating A^{-1} would be the preferred method in a BLUP evaluation in which bulls are grouped by American, Canadian, and dual nationality.

More bulls have entered AI service in both countries and exchange of semen has continued since completion of the evaluations used in this

study. However, the addition of more bulls to each population is not expected to affect the conclusion of this study, because the new bulls are descendants of the bulls examined. The bulls studied, therefore, still provide the genetic ties needed to conduct joint evaluation of bulls from both countries.

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