Impact of Genetic Correlations on Accuracy of Predicting Future Evaluations

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ABSTRACT

International evaluations for Holstein bulls were calculated by the International Bull Evaluation Service with data available in February 1995 from Canada, Denmark, France, Germany, Italy, Sweden, The Netherlands, and the US using current methodology with either correlations between countries of unity (0.995) or estimates of less than unity. To determine which of the two evaluation methods was most accurate, results of the two sets of evaluations for milk, fat, and protein yields for each country were compared with national evaluations in 1999. The 1999 national evaluations were assumed to be the best estimates of true genetic merit on a particular national scale. To reduce the impact of the part-whole relationship that results from earlier national data, a key part of the study was restricted to bulls with data from at least twice as many daughters for 1999 national evaluation as for 1995. Correlations and standard deviations of differences from later national evaluations showed no advantage to accounting for genetic correlations between countries. For bulls without national data in the earlier international evaluations and, therefore, no data in common with the later national evaluation, the advantage from using variable genetic correlations for yield was small. Thus, the use of variable genetic correlations had marginal value.
(**Key words:** genetic correlation, international evaluation, genetic evaluation)

Abbreviation key: Interbull = International Bull Evaluation Service, **I95** = Interbull evaluations calculated from February 1995 data using genetic correlations less than unity, **U95** = Interbull evaluations calculated from February 1995 data using genetic correlations of essentially unity, **N99** = national evaluations in 1999, $\mathbf{r_g}$ = genetic correlation, and **SD** = standard deviation.

INTRODUCTION

Accuracy in genetic evaluations is dependent on the correctness of the statistical parameters assumed. Estimates of genetic variances and genetic correlations (**r_g**) are incorporated into the evaluation procedures and have considerable impact on the ranking of bulls across countries for International Bull Evaluation Service [**Interbull** (1)] evaluations. Procedures to derive those estimates have been improved (1), but concern persists on the appropriateness of the r_g that are used.

Genetic correlations across countries can be less than unity because of 1) interaction between genotype and environment, 2) differences in trait definition, and 3) differences in national systems for genetic evaluation methodology. An interaction between genotype and environment is easily visualized: animals with certain genotypes are relatively better suited to withstand or to benefit from the weather, disease, or feed supplies of a certain geographical region than in another environment. Trait definition often is overlooked as a reason for genetic correlations of less than unity. Some national evaluations include only first lactation records, whereas evaluations from other countries include records from the first three or five parities or from an unlimited number of parities. Because r_g among lactations are less than unity, yield traits with the same name are not the same trait across all countries. Finally, variations in evaluation methodology affect bull ranking and contribute to estimates of genetic correlation less than unity. For illustration purposes, consider two evaluation systems that use the same data and the same trait but one system is so primitive or contains programming errors so that the resulting evaluations are random numbers; the estimated r_g between the two systems would be 0 even in the absence of an interaction between genotype and environment. Ironically, the top bulls for Interbull evaluations on the scale of the country with the evaluations that are random numbers would be only from that country's evaluation and, therefore, mostly local bulls.

National bull evaluations were initially combined into international evaluations by Interbull (1) using an r_g of near unity (0.995). In August 1995, the general system of evaluation (4) used by the Interbull Centre [Uppsala, Sweden (1)] remained, but the feature of variable r_g was employed, which resulted in a different ranking of bulls for each country.

The primary value of receiving Interbull evaluations is to obtain estimates of genetic merit for bulls that have semen available for marketing in a particular country but do not have national evaluations at that time. National and international evaluations at a given time have been compared in their ability to rank and to predict future national evaluations (2, 3). Ideally, the later national evaluations are of high accuracy and are based on different daughters compared with the earlier evaluations. In practice, data are not totally independent.

Application of genetic correlations has a substantial impact on ranking of top bulls even though correlations for all bulls may be high between evaluations that consider or ignore genetic correlations. Routine Interbull results for Holstein bulls in February 1999 showed 72, 48, and 60 USA Holstein bulls in the top 100 on the USA scales for milk, fat, and protein, respectively. Corresponding numbers of USA bulls on German scales were only 55, 25, and 39. From a breed improvement point of view, the merit of these groups of bulls may not differ markedly, but there is a tremendous marketing difference.

The objective of this study was to compare evaluations from combining data across countries either with or without r_g for the effectiveness of those evaluations in predicting future national evaluations. Also, the impact of considering r_g on selection of top bulls was studied.

MATERIALS AND METHODS

International evaluations of Holstein bulls that had been computed by the Interbull Centre from data used for February 1995 routine evaluations were calculated by the Interbull Centre with its current methodology but that included either a variable r_g of less than unity (**I95** evaluations) or an r_g of unity (**U95** evaluations). Because unique solutions could not be obtained with $r_g = 1$, an r_g of 0.995 was used to represent unity.

Nine countries provided data for the February 1995 Interbull evaluations, but because Finland did not have data for fat yield it was not included in this study. Results on the scales of Canada, Denmark, France, Germany, Italy, Sweden, The Netherlands, and the US were compared with 1999 national (**N99**) evaluations from each of those countries. The I95 evaluations were the same as the evaluations used by Powell et al. to compare national and Interbull evaluation in predicting later national evaluations (3). The r_g for I95 evaluations and the variances for I95 and U95 evaluations were those used for August 1995 Interbull evaluations. The r_g for I95 ranged from 0.87 to 0.96. Swedish evaluations were expressed in relative breeding values, which are reported as percentages. Danish evaluations were also in relative breeding values for 1995 but in breeding value (kg) for 1999. Therefore, they were included only for comparison of correlations but not measures of differences. Canadian evaluations were reported as transmitting abilities in units of breed class averages for 1995, but were changed to breeding value (kg), which is how Canadian evaluations currently are expressed. Evaluations were reported as transmitting ability for the US and as breeding values for the remaining countries.

The impact and effectiveness of the model with variable r_g for each country pair was examined by comparing I95 and U95 evaluations for milk, fat, and protein yields with corresponding N99 evaluations for each country. The number of bulls included in various data sets is shown in Table 1. All bulls had N99 evaluations in the particular country. Categories of bulls were defined for each country based on the situation for 1995. For each country, category 1 included bulls with data only from that country; category 2 included bulls with data also from another country; and category 3 included bulls without national data in 1995. Category 1 included all bulls that were not returned to AI service after initial progeny test as well as any other bulls without semen exported. Category 1 bulls did not contribute to the examination of r_g, but were included to provide a reference for the numbers of bulls in other categories relative to all bulls. For bulls in category 2, a part-whole relationship between 1995 international evaluations and N99 evaluations caused the I95 evaluations to be more related than were U95 with the N99 evaluations because the influence of foreign data was diminished for I95 evaluations compared with U95 evaluations. Bulls that did not add national data from 1995 to N99 would have a higher relationship between U95 and N99 even though I95 might be a superior predictor of true national merit. For bulls in category 2, the most meaningful results were from the subset that included only bulls where the number of daughters for N99 evaluations were at least twice the number of national daughters for 1995 international evaluations in an attempt to reduce the impact of this part-whole relationship. Category 3 bulls were completely free of any part-whole relationship distortion but could not be used to examine the relative accuracies in combining national and foreign data.

Comparisons were made by product-moment correlations and by standard deviations (**SD**) of differences between I95 or U95 evaluations and N99 evaluations. Higher correlations and lower SD for I95 would be evidence of improvement due to use of variable r_g. Although the genetic bases in Canada, Denmark, France, and Sweden had changed between national evaluations in 1995 and 1999, correlations and SD of differences should be unaffected. Changes in national evaluation methodology between 1995 and 1999 would make the conclusions less applicable but still useful.

RESULTS

Category 1 (bulls with daughters in only that country for 1995 international evaluations) had the most bulls (Table 1) and included from 72 to 96% of all bulls (sum of the three categories) for a particular country. The correlations between I95 and U95 evaluations for category 1 bulls were at least 0.9997 for each country. The high correlations verified that the evaluations were computed as expected.

Comparisons of correlations or SD of evaluation differences should be made within, not across, countries. Many factors affect the relationship between pairs of evaluations. Sets of evaluations will be more similar if the input data are more similar. For example, evaluations for bulls not increasing in amount of information (numbers of daughters and lactation records) would be highly related relative to evaluations for bulls adding data. Proportion of 1995 Interbull data composed of local data directly affected the relationship between I95 or U95 with N99. Changes (improvements) in national evaluation procedures from 1995 to 1999 would lower the relationship. Therefore, comparisons of correlations or SD of differences across countries is not valid. However, within country, higher correlations and lower SD of differences between 1995 and 1999 evaluations were assumed to indicate the merit of the methodology in regard to use of variable r_g. Even a comparison of the numbers of bulls requires caution. French evaluations of bulls that were not sampled there as young bulls are not included in Interbull evaluations. Therefore, the number of bulls in category 2 for France is much less than if data for all foreign bulls with daughters in France had been included in Interbull evaluations.

Because category 1 bulls were the most numerous for each country, correlations between I95 and U95 for all bulls were essentially unity. Despite high correlations, rankings of top bulls were often markedly changed, favoring home countries. For example, the number of US bulls in the top 100 on the US fat scale increased 14 (45 to 59) with the r_g considered while on the German scale decreasing 11 (42 to 31). Using the results from I95 as the standard, the means for the top 100 bulls selected on U95 instead of I95 decreased 2 to 17 kg EBV milk on the various national scales. Corresponding ranges for fat and protein decreases were .5 to .8 and .1 to .7 kg.

Correlations of N99 evaluations with U95 and I95 evaluations are in Table 2 for bulls in category 2 (data from at least one other country for 1995 international evaluations). Correlations with I95 evaluations were higher (i.e. variable r_g apparently useful) for 18 of 24 country-trait results. Corresponding SD of differences (Table 3) also generally favored (17 of 21 were smaller) I95 compared with U95 evaluation differences from N99 evaluations. For the six countries with evaluations in kilograms, SD's of differences from N99 evaluations based on breeding value were lower for I95 evaluations than for U95 evaluations by a mean of 12 kg of milk, .8 kg of fat, and 0.5 kg of protein. However, for Germany, SD of differences were essentially equal, and for Italy, SD of differences from N99 evaluations for milk and protein were lower for U95 evaluations than for I95 evaluations. These results for all category 2 bulls favor variable r_g but that is apparently due to part-whole relationships and not necessarily inherent merit as revealed in examinations described later.

The percentage of national data in 1995 international evaluations for bulls in category 2 was lowest for Denmark (4%) and Italy (17%) and highest for the US (58%). The smaller percentage of national data for Denmark and Italy likely explains the apparent lower benefit of variable r_g for bulls in category 2 (Tables 2 and 3), because the relationship between I95 and N99 evaluations was not as inflated as that for other countries by part-whole relationships.

To confirm that the part-whole relationships were accounting for some of the difference in results across countries, bulls in category 2 with an increase of <5% in national daughter numbers were studied (not shown in tables). For that subset, I95 evaluations were a better predictor of N99 evaluations relative to U95 evaluations than was shown in Tables 2 and 3 for bulls in category 2. Thus, when less new national data were added, the reduced impact of foreign data for $r_g < 1$ led to a closer relationship with later national evaluations. This increased similarity was attributed to increased part-whole relationships.

A separate examination was made for bulls in category 2 with twice as many domestic daughters from 1995 to 1999 because of concern that the part-whole relationship might distort conclusions from the previous comparisons. Correlations between evaluations for this subset are in Table 4 and SD of differences in evaluations are in Table 5. Numbers of bulls were reduced considerably (Table 1), but data for Canada, Germany, and the US still included evaluations from >50 bulls. Individual country results should be interpreted with consideration of the limited numbers of bulls. Correlations with N99 evaluations (Table 4) generally favored I95 (application of variable r_g) over U95 evaluations for Italy, Sweden, and the US (7 of 9 trait-country combinations). In contrast, most correlations for the other countries (13 of 15 trait-country combinations) were higher with U95 (r_g of unity) evaluations. Correlations with N99 evaluations for Canada were nearly equal for U95 and I95 evaluations. Correlations do not provide as useful information as do SD of evaluation differences because correlations only indicate how the bulls rank among that group and not how well evaluations of those bulls are estimated relative to evaluations for the full set of bulls in the national evaluation. Decreases in SD of differences from N99 evaluations were found for I95 evaluations compared with U95 evaluations for all three traits for the US, fat for Italy, and milk and protein for Sweden. Most SD for European countries were lower for U95 evaluations compared with I95 evaluations. Canada had similar SD for both international evaluation procedures. Overall no clear advantage was shown for either variable or unity r_g when national data had less of a part-whole relationship, although an r_g of unity tended to be favored. This occurred even though there was some remaining part-whole relationship that would favor I95.

No part-whole relationship existed for bulls in category 3 because no national data were included in 1995 international evaluations. Therefore, results for bulls in category 3 provide an opportunity for a second and independent examination of the relative merit of the use of r_g in improving the accuracy of genetic evaluation. For bulls in category 3, correlations with N99 evaluations (Table 6) were higher for U95 evaluations as often as for I95 evaluations and correlation differences generally were small. In Table 7, SD of evaluation differences from N99 evaluations were smaller for I95 evaluations than for U95 evaluations 14 times, equal 4 times, and larger 3 times. The actual differences were negligible. Mean reductions in SD on a breeding value (kg) basis were only 1.7 for milk, .23 for fat, and .07 for protein.

CONCLUSIONS

Impact on mean EBV of top bulls from ignoring r_g when considering r_g was assumed to be proper varied from inconsequential to likely important, 17 kg milk, .8 kg fat, and .7 kg protein. The apparent advantage for variable r_g in prediction of future national evaluations for bulls with data from at least one other country for international evaluations (category 2) was due to the part-whole relationship (inclusion of same daughters in 1995 and 1999 evaluations). Using subsets of bulls with data from at least twice as many domestic daughters in 1999 as in 1995 showed that there was no improvement in prediction due to r_g. Even with the doubling requirement, I95 evaluations still were at an advantage from the part-whole relationship because of the more limited impact of foreign data. Bulls without national data (category 3) were not affected by that part-whole relationship, and results for those bulls showed no advantage in correlations of evaluations from either international method with later national evaluations. The SD of differences favored use of $r_g < 1.0$, but reductions in SD were minor. The use of variable r_g did not improve the prediction of future national evaluations for bulls in category 2 and showed only a slight improvement for bulls in category 3.

This overall conclusion on the impact of r_g on accuracy of genetic evaluations may not apply to every country pair. Unfortunately, the two countries with the lowest current r_g with most other countries, Australia and New Zealand, did not have 1995 international data and, therefore, were not included in the study. However, two other countries with relatively low r_g with other countries (0.87 for Germany and 0.90 for Denmark and Sweden with the US) were included, and comparing their results to those from the other countries with higher r_g provided no evidence that would suggest that the inclusion of countries with even lower r_g would alter conclusions.

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Table 1. Numbers of Holstein bulls with data from only that country (category 1), from that country and at least one other country (category 2), and without national data (category 3) for 1995 international evaluations.

		Category 2		
Country of scale	Category 1	All bulls	Subset[1]	Category 3
	(no.)	(no.)	(no.)	(no.)
Canada	1463	315	59	258
Denmark	2620	42	8	59
France	3040	129	19	397
Germany	2034	227	60	333
Italy	1188	206	44	245
Sweden	894	103	18	87
The Netherlands	2739	271	32	276
US	10,429	605	77	305

[1]Bulls with at least twice as many daughters for 1999 national evaluations as for 1995 international evaluations.

Table 2. Correlations of 1999 national (N99) evaluations for yield traits and international evaluations with genetic correlations as estimated (I95) or unity (U95) for February 1995 data for Holstein bulls with data included in the international evaluations along with data from at least one other country (category 2).

	U95 and N99 evaluations			I95 and N99 evaluations		
Country	Milk	Fat	Protein	Milk	Fat	Protein
Canada	0.934	0.916	0.931	0.939	0.925	0.938
Denmark	0.930	0.925	0.934	0.926	0.937	0.933

France	0.947	0.931	0.936	0.955	0.948	0.951
Germany	0.921	0.922	0.930	0.923	0.919	0.926
Italy	0.918	0.940	0.925	0.908	0.951	0.914
Sweden	0.834	0.765	0.793	0.852	0.780	0.820
The Netherlands	0.968	0.965	0.968	0.980	0.980	0.982
US	0.961	0.959	0.961	0.971	0.970	0.972

Table 3. Standard deviations[1] of differences of 1999 national (N99) evaluations for yield traits from international evaluations with genetic correlations as estimated (I95) or unity (U95) for February 1995 data for Holstein bulls with data included in the international evaluations along with data from at least one other country (category 2).

	N99 – U95 evaluations			N99 – I95 evaluations		
Country	Milk	Fat	Protein	Milk	Fat	Protein
Canada, kg	294	11.6	8.6	280	10.8	8.0
France, kg	202	8.5	6.2	186	7.4	5.4
Germany, kg	200	7.6	5.3	199	7.7	5.4
Italy, kg	187	5.9	5.6	201	5.2	6.0
Sweden, %	3.5	3.6	3.3	3.3	3.4	3.2
The Netherlands, kg	157	5.5	4.5	130	4.4	3.5
US, kg	100	3.5	2.9	87	3.0	2.5

[1]Transmitting ability for US; breeding value for other countries.

Table 4. Correlations of 1999 national (N99) evaluations for yield traits and international evaluations with genetic correlations as estimated (I95) or unity (U95) for February 1995 data for Holstein bulls with data included in the international evaluations along with data from at least one other country (category 2) and with at least twice as many daughters for N99 evaluations as national daughters for 1995 international evaluations.

	U95 and N99 evaluations			I95 and N99 evaluations		
Country	Milk	Fat	Protein	Milk	Fat	Protein
Canada	0.908	0.893	0.902	0.897	0.891	0.900
Denmark	0.976	0.865	0.960	0.952	0.965	0.946
France	0.890	0.828	0.851	0.866	0.830	0.833

Germany	0.882	0.898	0.894	0.867	0.871	0.865
Italy	0.830	0.912	0.840	0.838	0.927	0.839
Sweden	0.752	0.863	0.676	0.802	0.859	0.732
The Netherlands	0.932	0.944	0.925	0.907	0.935	0.897
US	0.928	0.898	0.923	0.939	0.914	0.931

Table 5. Standard deviations[1] of differences of 1999 national (N99) evaluations for yield traits from international evaluations with genetic correlations as estimated (I95) or unity (U95) for February 1995 data for Holstein bulls with data included in the international evaluations along with data from at least one other country (category 2) and with at least twice as many daughters for N99 evaluations as national daughters for 1995 international evaluations.

	N99 – U95 evaluations			N99 – I95 evaluations		
Country	Milk	Fat	Protein	Milk	Fat	Protein
Canada, kg	280	11.6	8.4	292	11.6	8.3
France, kg	264	11.5	8.3	287	11.6	8.7
Germany, kg	229	8.4	6.6	241	9.3	7.1
Italy, kg	201	6.2	6.5	207	5.7	7.0
Sweden, %	4.0	4.3	4.2	3.7	4.6	3.8
The Netherlands, kg	147	5.7	4.6	182	6.6	5.5
US, kg	123	4.8	3.4	113	4.5	3.2

[1]Transmitting ability for US; breeding value for other countries.

Table 6. Correlations of 1999 national (N99) evaluations for yield traits and international evaluations with genetic correlations as estimated (I95) or unity (U95) for February 1995 data for Holstein bulls with no data included in the international evaluations (category 3).

	U95 and N99 evaluations			I95 and N99 evaluations		
Country	Milk	Fat	Protein	Milk	Fat	Protein
Canada	0.697	0.748	0.730	0.695	0.747	0.725
Denmark	0.865	0.826	0.887	0.871	0.826	0.886
France	0.827	0.791	0.810	0.825	0.796	0.809
Germany	0.827	0.815	0.830	0.817	0.813	0.824

Italy	0.888	0.808	0.873	0.889	0.813	0.873
Sweden	0.751	0.634	0.668	0.756	0.653	0.681
The Netherlands	0.898	0.840	0.880	0.896	0.842	0.879
US	0.895	0.863	0.893	0.898	0.866	0.896

Table 7. Standard deviations[1] of differences of 1999 national (N99) evaluations for yield traits from international evaluations with genetic correlations as estimated (I95) or unity (U95) for February 1995 data for Holstein bulls with no data included in the international evaluations (category 3).

	N99 – U95 evaluations			N99 – I95 evaluations		
Country	Milk	Fat	Protein	Milk	Fat	Protein
Canada, kg	515	18.0	15.2	505	17.9	14.9
France, kg	403	15.8	11.9	403	15.4	11.9
Germany, kg	412	14.1	11.4	426	14.2	11.6
Italy, kg	308	12.7	10.3	304	12.3	10.3
Sweden, %	6.3	5.9	6.2	6.1	5.6	5.9
The Netherlands, kg	279	11.6	8.2	271	11.2	7.9
US, kg	183	7.4	5.6	182	7.3	5.6

[1]Transmitting ability for US; breeding value for other countries.