Factors Affecting Calculation and Use of Conversion Equations for Genetic Merit of Dairy Bulls

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ABSTRACT

Factors affecting calculation and use of conversion equations were reviewed. Methods of expressing reliability of converted evaluations were surveyed. Of 16 countries responding, 6 did not calculate reliability for converted evaluations, 5 accepted reliability from the exporting country, and 5 assumed genetic correlations of .6 to 1.0 with the US. Genetic correlations between the US and 8 other countries were estimated and generally were ≥.9; estimated correlations between the US and Canada were 1.0. Estimated correlations averaged .93 for milk, .89 for fat, and .92 for protein yields. Correlation estimates were lowest for countries differing most from the US in management conditions (Australia, New Zealand) or trait definition (Germany), which suggests that correlation estimates <1.0 indicate differences in trait measurement as well as differences in biological expression. Conversion equations were computed from data of US and Canadian Holstein bulls with and against the gene flow. Equations against the gene flow generally had regression coefficients and intercepts lower than those calculated with the gene flow. Lower regression coefficients were explained by selection on the dependent variable. Lower intercepts were attributed to preferential treatment of daughters from imported semen, which would lower intercepts for equations against the gene flow and inflate intercepts with the gene flow.
(**Key words**: genetic merit, bias, preferential treatment, conversion)

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Abbreviation key: DYD = daughter yield deviation, **INTERBULL** = International Bull Evaluation Service, $\mathbf{r_g}$ = genetic correlation, $\mathbf{r_p}$ = product-moment correlation, **REL** = reliability, $\mathbf{REL_c}$ = REL of converted evaluation, $\mathbf{REL_e}$ = REL in exporting country.

INTRODUCTION

International trade of dairy bull semen is increasing. Proper breeding choices require estimates of bull merit across countries. Philipsson (7) described the background of international efforts, including the establishment of the International Bull Evaluation Service (INTERBULL). The Goddard and Wilmink procedures for developing conversion equations were recommended by INTERBULL, and these two methods have been described and compared (8). Both procedures require evaluations for the same group of bulls in both countries.

Conversion Equations

The three major concerns regarding the accuracy of conversion equations have been 1) preferential mating of foreign bulls, 2) preferential treatment of resulting daughters, and 3) appropriateness of the sample. Adoption of animal model procedures have largely eliminated the problem of preferential mating. Some evaluation systems have features that may reduce the impact of preferential treatment, such as consideration of interaction of herd and sire (13) and heterogeneous variance (14) or definition of management groups separately by registration status (13), but these efforts can be only partially effective. In many situations, particularly with breeds other than Holstein, data are insufficient to provide clearly defensible equations. To obtain as many paired evaluations as possible, data often include a longer time than desirable, evaluations with lower reliabilities (**REL**) are accepted, or data from gene flow in both directions are combined. Equations to convert from an importing country to the exporting country often are computed only from data against the gene flow.

Recommendations by INTERBULL (4) on which bulls should have data included in computing conversion equations are 1) a birth year during the last complete 10 yr of bull births, 2) REL of ≥75%, and 3) daughters in ≥20 herds. The birth year requirement was included because of concern that genetic evaluation systems differ in how fully they account for genetic trend. If data are available for a sufficient number of bulls, only bulls initially sampled in the exporting country should be included. If, based on these recommendations, <20 bulls qualify, a theoretical approach should be used for development of conversion equations. With the theoretical method, the regression coefficient (b value) is computed from population variances and mean REL. The intercept (a value) depends on the bulls in common.

Schaeffer (11) suggested applying a linear model to daughter deviations from bull evaluations in multiple countries. This method combines daughter data across countries and links data through male relationships. Resulting evaluations are on a common scale so that application of conversion equations is not needed for bulls with data included. However, regression coefficients, which are obtained from ratios of population standard deviations, are needed in advance of analysis. Conversion equations for bulls that are not in the analysis but that are from included countries use those regression coefficients and intercepts from country solutions. Because of preferential treatment, Banos (1) recommended that the approach of Schaeffer (11) be modified to ignore daughters that result from imported semen. Thus, each bull would have daughter data included only from the country of initial sampling. The linear model method was promoted as having the advantage of using daughter data from all countries. To use only data from the first country would sacrifice that advantage to remove the impact of preferential treatment. Use of male relationships still ties evaluations across countries.

A major weakness of these linear model approaches is the need to assume that the genetic correlation (**r_g**) is 1.0. Biologically, traits may be similar or even identical across countries (environments), but their measurement may be so different that effective r_g is <1.0. An advantage of the Goddard and Wilmink methods is that they are based on the relationship between evaluations in the two countries and automatically account for effective r_g regardless of magnitude. Preferential treatment and $r_g \neq 1.0$ are the primary reasons why conversion equations are not reciprocal. Schaeffer (12) has proposed an approach that treats evaluations in different countries as correlated traits and, thus, allows for $r_g \neq 1.0$.

Computer and human resources and availability of data determine which conversion methods are used. The Goddard and Schaeffer methods require unregressed daughter data such as daughter yield deviations (**DYD**). If DYD are not available, approximations are necessary, or, if only two countries are involved, the Wilmink method is appropriate. Powell and Sieber (8) have shown that the Goddard method is more accurate than the Wilmink method. In addition, the Goddard method is easier to understand, to explain, and to compute and is more appropriate if ancestral input in the second country is incomplete, as is the usual case. The basis for multiplying the exporting country's evaluation by the importing country's REL is not obvious for the Wilmink method. For computation of Goddard equations, such calculations are not needed, and the intercept is obtained directly rather than through the regression coefficient and the means for the evaluations of the two countries. Because the unregressed daughter data are used, the Goddard method is independent of parent data in the importing country. The parent average information in the importing country often is based on limited data and may even be represented by unknown-parent solutions. Inaccurate parent average information directly affects equations from the Wilmink method. Nonetheless, the Wilmink method has been used widely and appropriately when DYD were not available.

Conversion methods are dependent not only on the kind of data available, such as DYD, but also on the existence of data. In France, a bull evaluation is not released if the bull has a foreign evaluation calculated prior to the bull's use in France. In the absence of evaluations for the same bulls in two countries, neither the

Goddard nor Wilmink methods can be applied. French researchers (6) have developed intercepts using data from full brothers in France and the US and regression coefficients from population variances. With the use of young US bulls in France, concerns about preferential treatment and other errors are reduced, and these simultaneously sampled bulls should allow utilization of the Goddard method.

Major factors affecting size of intercepts are mean of true genetic differences between populations and relative currentness of base definitions. Currentness cannot be determined by base date alone because that date might refer to different events or genders. Obvious factors that affect size of regression coefficients are physical measures (e.g., pounds vs. kilograms) and genetic measures (e.g., breeding value vs. transmitting ability). More subtle factors are the bases for age adjustment and for consideration of heterogeneous variance, the assumed heritability, the completeness of the evaluation model, and the effective r_g.

Results of a simulation study (2) showed that direction of gene flow relative to direction of the conversion equation was not important in the absence of selection. However, with selection, computation of conversion equations against the gene flow reduced regression coefficients because of selection on a trait that is treated as the dependent variable. Intercepts and regression coefficients usually move in opposite directions, and the intercept was inflated with selection. Because that inflation more than offset the lower regression coefficient, conversion equations computed against the gene flow resulted in evaluations that were mostly biased upward. However, for the highest bulls, the bias was negative.

International Rankings

The linear model method of combining data across countries produces bull evaluations on a common scale. Conversion equations, although used primarily to predict merit of individual bulls, can also place evaluations for bulls from a number of countries on the same scale. Countries can then be ranked as sources of genetics. Although means for countries are of some interest, primary emphasis would be on location of the top bulls, not only for immediate use, but also to indicate likely sources of future top bulls. Currentness of data varies across countries, and some countries have a relative advantage because of genetic trend. However, if data are reasonably comparable in time, bias because of genetic trend can be minimized. Differences in amount of information required to attain a specified minimum REL also affect a country's ranking on combined lists. Countries in which that minimum is reached with less data have an advantage because more bulls, especially young ones, qualify than in a country with more conservative REL. Practices for editing data also should be considered for interpretation of combined lists of national and converted evaluations. For example, a list might contain only those bulls from other countries that are marketed in the importing country. Such a list of available bulls is pertinent to breeders in that country but can be misleading to others for whom that restriction is not appropriate.

The use of conversion equations can readily be criticized because some bulls differ markedly in their evaluation in one country and their converted evaluation from the other country. Although biased data in either country contribute to differences, differences for individual bulls can be large because converted evaluations are based on data that are completely separate from those used for national evaluations. Users of genetic data usually are accustomed to comparison of current and past evaluations, but past evaluations are based on a subset of the data included in current evaluations. Comparison of national and converted evaluations is similar to comparison of an early evaluation of a bull with a later evaluation that was based only on information from additional daughters and on new information for parents and other relatives. On average, differences between evaluations and converted evaluations are essentially 0 for the group of bulls used for development of the equations. Emphasis of a few individual observations that deviate from the regression represented by the conversion equation is inappropriate and retards genetic progress.

Accuracy of a converted evaluation depends on REL of the evaluation in the exporting country (**REL$_e$**), on the r_g, and on the accuracy of the equations developed from a finite sample of data. The INTERBULL recommendation (4) is to estimate REL for the converted evaluation (REL_C) as $REL_C = REL_e(r_g^2)k$, where k is a factor to account for inaccuracy in the conversion equations.

Research objectives were 1) to survey countries to determine the expressions of REL_C, 2) to provide estimates of r_g, and 3) to examine the effect of determining conversion equations against the gene flow.

MATERIALS AND METHODS

Survey on REL_C

Seventeen countries were surveyed on expression of REL_C (Table 1). Responses were summarized, categorized, and returned to providers to review for correct interpretation.

Estimation of r_g

Genetic evaluation files from eight countries were provided to the US. The pairing of evaluations allowed the calculation of product-moment correlations (r_p) between corresponding traits and collection of REL information needed to estimate r_g according to the procedure of Calo et al. (3):

$$r_g = r_p/[REL_e(REL_i)]^{.5},$$

where REL_i is REL in the importing country. This method has been used widely to compute r_g and to compute the expected r_p for an assumed r_g (often 1.0) for comparison with the actual r_p. Because of genetic trend, use of data across years inflates estimates of r_p. Therefore, r_p was computed within birth year by fitting of each country's evaluations with a model that contained birth year and by correlation of residuals.

Conversion Against the Gene Flow

Data from US and Canadian bulls were sufficient to compute conversion equations in both directions (with and against the gene flow) and to enable empirical comparison. Evaluations from January 1993 were used for bulls with a birth year of ≥1975, an REL of ≥75%, and daughters in ≥20 herds. Bulls were categorized according to country of first sampling. Bulls were designated as US if they had a US controller (US file) and entered AI service at 7 to 39 mo of age or had daughters in >100 herds. Bulls were designated as Canadian if they had a Canadian owner (Canadian file) and if the first daughter calved in Canada 3 to 5 yr after the bull's birth. Bulls that met requirements for both countries were excluded so that data would not overlap and so that effect of direction of gene flow could be examined most effectively. Final data included 158 US bulls and 153 Canadian bulls. Canadian evaluations routinely contribute to US national evaluations (15), but the US evaluations in this study were from a research file with evaluations based only on US data.

Conversion equations to estimate PTA for the US were computed with Goddard and Wilmink methods. Equations to estimate Canadian breed class averages were computed with the Wilmink method. Equations were computed for milk, fat, and protein yields. Limits on REL and herds were applied separately for

TABLE 1. Results of an international survey on expression of reliability (REL) assigned to converted evaluations (REL_C).

Expression of REL_C	Country	r_g[1]
No specific calculation or recommendation	Canada	
	Finland	
	Israel	
	Spain	
	Sweden	
	US[2]	
AcceptREL_e[3] as REL_C	France	
	Germany	
	Greece	
	Italy	
	The Netherlands	
$REL_e(r_g^2)$	Australia	.80
	Austria[4]	.86
	Ireland	.92
	New Zealand[5]	.60
	United Kingdom	.92
$REL_e(r_g^2)k$[6]	Denmark[7]	1.0
No response to survey	Norway	

[1]r_g = Genetic correlation.

[2]For converted Canadian evaluations incorporated into USDA evaluations, REL_e is adjusted to reflect equivalent amount of US information, and an r_g = 1.0 is assumed.

[3]REL from the exporting country.

[4]r_g for conversion of US evaluations.

[5]In practice, REL_C = .35.

[6]Where k is a factor of .93 to account for inaccuracy.

[7]In practice, $REL_C = REL_e - .07$.

protein, which reduced the number of bulls to 150 for those first evaluated in Canada.

RESULTS AND DISCUSSION

Survey on REL_c

Survey results on the expression of REL_c are in Table 1. More than half of the respondents either do not make a recommendation as to the accuracy of converted evaluations or accept REL_e. Other replies indicate a variety of calculations. Australia, Austria, Ireland, New Zealand, and the United Kingdom all consider an r_g of <1.0. Although that approach is recommended by INTERBULL (4), a factor to account for inaccuracy of the conversion process is not included. The most limiting situation is that for New Zealand, where all converted evaluations in practice are given an REL_c of .35.

Data from the exporting country were combined with national data in many countries (Australia, Austria, Ireland, New Zealand, the United Kingdom, and the US). The US provides an REL_c only for bulls from Canada and combines US and Canadian data for Canadian bulls when possible (15). The difference in algorithms for calculation of REL in the US and Canada is considered in quantification of the amount of information in terms of US daughter equivalents before Canadian data are incorporated into US evaluations.

Estimation of r_g

Estimated r_g between the US and 8 countries are in Table 2 for milk, fat, and protein yields. For all yield traits, essentially $r_g = 1$ between the US and Canada. Such high correlations were expected because the Canadian evaluation system is more similar to that of the US than are evaluation systems of other countries, except the United Kingdom. However, previous research using the same starting data resulted in evaluations that were much less similar than expected for Ayrshires and Jerseys (9, 10). The evaluation system of the United Kingdom was adapted from that of the US, which perhaps contributes to the r_g estimate of

TABLE 2. Estimated genetic correlations (r_g) calculated from reliabilities (REL) in the US and in the other country and from the product-moment correlation (r_p) from data used to compute US conversion equations.

Country	Yield trait	Number of bulls	REL: US	REL: Other	r_p	r_g
Australia	Milk	43	.960	.901	.804	.864
	Fat	43	.960	.901	.738	.794
	Protein	43	.957	.901	.774	.834
Canada	Milk	158	.893	.976	.931	.997
	Fat	158	.893	.976	.946	1.013
	Protein	158	.888	.976	.930	.999
Denmark	Milk	57	.981	.931	.834	.870
	Fat	57	.981	.931	.797	.831
	Protein	57	.978	.932	.878	.920
Germany	Milk	78	.878	.917	.730	.814
	Fat	78	.878	.917	.759	.846
	Protein	78	.865	.917	.696	.781
Italy	Milk	240	.988	.955	.874	.900
	Fat	240	.988	.955	.872	.898
	Protein	240	.988	.955	.868	.894
The Netherlands	Milk	111	.964	.947	.855	.895
	Fat	111	.964	.947	.884	.925
	Protein	111	.962	.947	.877	.919
New Zealand	Milk	45	.942	.858	.806	.897
	Fat	45	.942	.858	.809	.900
	Protein	45	.935	.848	.759	.852
United Kingdom	Milk	69	.964	.962	.921	.956
	Fat	69	.964	.962	.915	.950
	Protein	69	.962	.962	.916	.952

TABLE 3. Intercepts (a) and regression coefficients (b) for predicting US or Canadian Holstein evaluations from evaluations in the other country using data for bulls initially sampled in the exporting country (with gene flow) or in the importing country (against gene flow) with the Wilmink or Goddard method (8).

Country conversion	Gene flow direction	Trait	Number of bulls	Conversion method: Wilmink a	Wilmink b	Goddard a	Goddard b
				(kg)	(kg/BCA[1] point)	(kg)	(kg/BCA point)
Canada to US	With	Milk	153	−30	54.8	−21	51.2
		Fat	153	1.6	1.82	2.0	1.68
		Protein	150	−.7	1.64	−1.0	1.51
	Against	Milk	158	−26	48.3	−22	48.1
		Fat	158	2.7	1.67	2.9	1.66
		Protein	158	−1.0	1.43	−1.7	1.44
				(BCA point)	(BCA point/kg)		
US to Canada	With	Milk	158	1.46	.0186	...	...
		Fat	158	−.83	.542	...	...
		Protein	158	1.24	.648	...	...
	Against	Milk	153	.54	.0182	...	...
		Fat	153	−.94	.566	...	...
		Protein	150	.44	.624	...	...

[1]Breed class average.

.95. Estimates of r_g were lowest for Australia (.83) and Germany (.81). The traits were probably most different for Germany, where management groups include herds from similar regions and with similar yields and where yield is treated as a combination of five traits: first lactation subdivided into three 100-d intervals, second lactation, and third lactation (5). Management conditions were most different from the US for Australia and New Zealand; therefore, lower r_g might be expected.

A limitation of the method used to estimate r_g was the different expressions of REL. Exact prediction error variances were unknown, and approximation procedures varied among countries. The REL may have been based on information from all relatives or only from daughters. The assumed heritability and the procedure to estimate REL also could have affected its size. For example, Canadian REL (called repeatability) for a given amount of information is higher than REL for the US, even after the higher heritability used in Canada (.33 vs. .25) is considered (15). To combine US and Canadian information, Wiggans et al. (15) reduced daughter equivalents by 10% for Canadian data. Thus, imprecise estimates of r_g could have resulted from inexact calculation of REL.

Conversion Against Gene Flow

Both Goddard and Wilmink methods were used to develop equations to convert Canadian evaluations to US equivalents (Table 3). The intercepts were usually higher by the Goddard method, and the regression coefficients were higher by the Wilmink method. Of primary interest was the comparison of intercepts and regression coefficients according to direction of gene flow. In nearly all cases, regression coefficients were lower for equations calculated against the gene flow, in agreement with the simulation results of Banos (2) and as expected because of selection. Regression coefficients calculated with the gene flow should be unbiased; if calculated against the gene flow, they are biased downward. In contrast to the simulation results (2), calculation of conversion equations against the gene flow generally reduced, rather than increased, the intercepts. Inflation of intercepts by reduction of regression coefficients against the gene flow was more than compensated for by some other factor that was present in the empirical data, but not in the simulation. When subsets of the data with 90% REL and repeatability were analyzed, all regression coefficients and intercepts were reduced when they were calculated against the gene flow.

Preferential treatment of daughters resulting from imported semen may cause the discrepancy between simulation and empirical results for intercepts. For example, if equations are computed for evaluations in the US from bulls initially used and evaluated in Canada (with the gene flow), the intercepts are inflated if daughters in the US receive preferential treatment. Equations that are from Canada to the US but that are calculated against the gene flow are based on bulls initially used in the US and later in Canada. If daughters in Canada are given preferential treatment, the resulting intercepts are lower. Thus, preferential treatment of daughters from imported semen inflates the intercept with the gene flow and reduces it against the gene flow.

The linear model approach, which ignores daughters except from the original country, also eliminates preferential treatment resulting from imported semen. If equations to predict evaluations of foreign bulls were unbiased by preferential treatment, those equations would routinely underestimate the eventual evaluation in the second country in the presence of preferential treatment. Such a situation presents an educational challenge because the prior assumption was that conversions are intended to be the best predictions of actual evaluations in the second country but did not consider that the actual evaluations might be biased.

CONCLUSIONS

Assumptions concerning REL_c varied considerably among countries. More than half of the survey respondents made no recommendation or accepted REL_e as REL_c. For other countries, assumptions of r_g with the US ranged from .6 to 1.0. Estimates of r_g calculated from r_p and from mean REL were generally ≥.85; for Canada, estimated r_g was 1.00. Across countries, mean estimated r_g were .90 for milk yield and .89 for fat and protein yields. Estimated r_g were lower for those countries that differ the most from the US in management conditions (Australia and New Zealand) or trait definition (Germany), which supports the suggestion that estimates of r_g <1.0 may indicate differences in trait measurement and differences in biological expression of the same trait.

Conversion equations calculated against the gene flow should be avoided. If sufficient data with the gene flow exist, they should not be combined with data against the gene flow. However, data with the gene flow may not exist or may be so sparse that the only practical way to develop conversion equations with acceptable sampling variation is to use data against the gene flow, even if that use results in biased conversions. Equations calculated from data against the gene flow generally had regression coefficients and intercepts that were lower than those calculated with the gene flow. Lower regression coefficients were explained by selection on the dependent variable. Lower intercepts were attributed to the preferential treatment of daughters resulting from imported semen. Such bias lowers intercepts for equations from data against the gene flow and inflates intercepts with the gene flow. Procedures that ignore potentially biased data are being researched by INTERBULL.

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