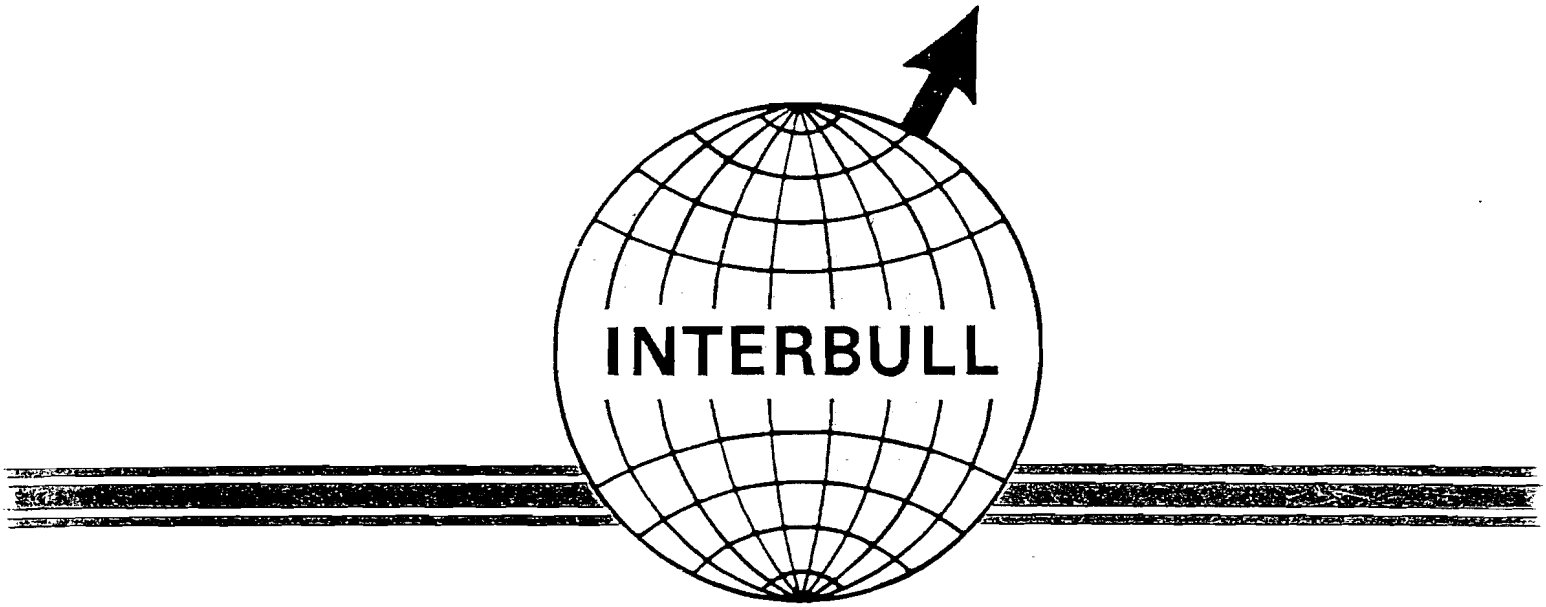

GENETIC CORRELATIONS BETWEEN COUNTRIES FOR SOMATIC CELL COUNT AND CONFORMATION TRAITS

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Contents

Genetic correlations between countries for somatic cell count and conformation traits

Abstract

Genetic correlations between countries were estimated for somatic cell count and 8 linear scored conformation traits. Data were the most recent Holstein bull evaluations for somatic cell count from Denmark, Finland and USA and for the conformation traits from Denmark, Canada and USA. A multiple trait model was used in which (de-regressed) proofs of bulls in different countries were considered to be different traits. Observations were within country de-regressed national proofs. An approximate EM-REML procedure was used to estimate genetic correlations between countries (=traits). For the conformation traits an international evaluation was run, using the estimated genetic correlations between countries.

Genetic correlation for somatic cell count ranged between 0.56 and 0.85 and for the conformation traits between 0.55 and 0.95. Comparison with proof correlations for sires with multiple proofs showed an underestimation of genetic correlations for somatic cell count, probably caused by lack of genetic ties between countries. Estimates of genetic correlations for conformation traits agreed better with proof correlations. Estimates of genetic correlation based on a multivariate model (using data of all countries) were lower than estimates based on a bivariate model (using data of only two countries).

An international evaluation with estimated genetic correlations showed different rankings between countries compared to a genetic correlation of unity, where differences in rankings between countries were small. Using estimated genetic correlations local bulls ranked higher than 'converted' bulls, compared to a genetic correlation of unity.

1 Introduction

Extensive exchange of dairy cattle germ-plasm (semen, embryos, live animals) currently takes place between countries and prompted the need for accurate bull comparisons. At present this problem is addressed by converting evaluations from the exporting country to figures equivalent to evaluations in the importing country (Goddard, 1985; Wilmink *et al.*, 1986). Analyses using conversion formulas suffer from several limitations, including a) the small number of sires used jointly, b) the potentially biased evaluations in the importing country that are based on imported semen due to preferential treatment of daughters of imported sires, and c) the allowance of only pairwise comparisons. One important advantage of these methods is that they account for genetic correlation less than unity between traits measured in the importing and exporting countries.

Schaeffer (1985) introduced a linear model comparison (LMC) procedure, which combines information from different countries, in form of national proofs, analyzes them with a linear model, and obtains an international estimate of the bulls' genetic merit. The assumption of unit genetic correlation is necessary, and the genetic evaluation methods of each participating country are assumed to remove as much bias from non-random mating and preferential treatment as is technically possible. Besides, the LMC method allows usage of only one heritability for all countries. Schaeffer and Zhang (1993) extended the LMC procedure such that evaluations within each country could be considered as separate traits with genetic correlations less than one and different variance ratios; multi-trait across country evaluation (MACE).

To date international genetic evaluation studies in dairy cattle have considered only production traits. However, availability of international genetic evaluations for additional traits would better serve breeding goals around the world. Problems often associated with additional traits are lacking records in some countries and differenct trait definitions among countries (Banos and Sigurdsson, 1994).

Aim of this study is to estimate genetic variances and covariances between Nordic countries and Canada and the United States of America as intermediate countries for conformation traits and somatic cell counts in Holstein bulls, using the MACE procedure.

2 Material and Method

2.1 Data

Data were the most recent Holstein bull evaluations for somatic cell count (SCC) from Denmark (DNK), Finland (FIN) and USA and for 8 linear scored conformation traits from Denmark (DNK), Canada (CAN) and USA. Bulls were born between 1950 and 1990. Proofs obtained in both country of first sampling of the bull and importing countries were included. Proofs were required to be based on more than 5 daughters. For the somatic cell count data set, 1 664 bulls had Danish, 1 228 bulls had Finnish and 18 163 bulls had US bull evaluation. Of these evaluations, 17 bulls had evaluations in both Denmark and Finland, 97 in Denmark and USA and 22 in Finland and USA. Total number of bulls in this data set was 16 271. The conformation traits data set consisted of 4 479 Canadian, 1 639 Danish and 14 671 US bull evaluations. Of these evaluations, 70 bulls had evaluations in both Canada and Denmark, 605 in Canada and USA and 74 in Denmark and USA. Total number of bulls in this data set was 20 118. For standarization only INTERBULL defined traits were used in the analysis. The appendix contains an overview of the by INTERBULL defined conformation traits that were investigated, and the related traits in the three different countries.

The first step involved the creation of an international database with respect to bull pedigree and national evaluation information. Initially two Nordic countries provided data on Holstein bulls: Denmark and Finland. Since these countries have made substantial imports form North America and to provide genetic links between countries data of USA and Canada were also included. To deal with the problem that a bull may have various registration numbers in different countries, a cross reference table constructed by INTERBULL is used to identify the bull uniquely by its identification in his first country of registration. In Table 1 the number of bulls with pedigree information provided by each country for both somatic cell count and conformation traits is shown.

The relationship matrix is assumed to provide ties among bulls from different countries. To get an impression of the strength of the ties among the participating countries, Table 2 shows the number of bulls from other countries that were found in pedigree files of the participating countries. Most exchange of semen occurred between Nordic countries and between North American countries, while export from North America to the Nordic countries provided genetic links between the two continents.

Table 1: Number of bulls and missing pedigree information per data set

	Somatic cell count			Conformation traits		
	DNK	FIN	USA	CAN	DNK	USA
Number of bulls	1664	1315	13848	4479	1637	14671
Missing birth year	0	0	0	0	0	1584
Missing sire	0	0	0	0	1	1572
Missing dam	0	0	0	1	0	1573
Missing mgs	6	0	9	136	6	1573
Missing mgd	1454	0	652	371	1455	1646

Table 2: Number of bulls from other countries found in pedigree files of participating countries for the somatic cell count and conformation traits data sets.

Other countries	Participating countries					
	Somatic cell count			Conformation traits		
	DNK	FIN	USA	CAN	DNK	USA
CAN	59	8	153	428	54	128
DEU	33	3			22	
DNK	95	18			79	
FIN		157				
FRA	1				1	
ITA	1				1	
NLD	11	26				
NZL	1					
SWE	3	130			1	
USA	239	82	1247	608	242	1168

Bull pedigree records included the identification of sire, dam, maternal grandsire and maternal granddam. Information about national origin of ancestors was used to determine the national origin of each bull as follows: one-half the origin of the sire plus one-quarter the origins of the maternal grandsire (MGS) and maternal granddam (MGD). Thus only unknown parents need to be assigned to genetic groups. Separate phantom parents groups for sires, MGS and MGD are recommended, because of the different selection intensities that could be applied to each group (Schaeffer, 1994). Genetic groups were also defined based on country of origin and year of birth, which in essence followed the idea of Westell *et al.* (1988) of phantom parent grouping.

2.2 Statistical model

The next step concerned the within country de-regression of the national proofs, followed by the estimation of genetic correlations, necessary for the international evaluation of the traits. To evaluate de-regressed national proofs from different countries the following model was used (Schaeffer, 1994):

$$y_i = \mu_i 1 + Z_i Q g_i + Z_i s_i + e_i \qquad (1)$$

where: y_i : vector of unregressed proofs from the i^{th} country;

μ_i : scalar for the i^{th} country;

g_i : vector of genetic group effects of phantom parents;

s_i : vector of random sire transmitting abilities for the i^{th} country, var(s) = A*G, A: bull additive genetic relationship matrix, G: trait genetic (co)variance matrix;

e_i : vector of residual effects in the i^{th} country; var(e) = R*e_i, R: diagonal matrix with diagonals equal to the reciprocal of the total number of daughters in a proof;

Z_i : matrix that relates proofs to sires;

Q : matrix that relates sires to phantom parents groups.

Unregressed proofs were computed within country from the national proof as follows:

$$y = R[A^{-1}k - A^{-1}kQ(Q'A^{-1}kQ)^{-1}Q'A^{-1}k + R^{-1}]P \qquad (2)$$

where k is the residual to sire variance ratio in each country, calculated as $(4-h^2)/h^2$, where h^2 is the heritability used in the national evaluation. Equation 2 can be derived from modified mixed model equations (Quaas and Pollak, 1981) pertaining to model 1. This precoede not only produces de-regressed proofs, but also renders estimated sire variances, necessary for building the MME pertaining to model 1. Because effective number of daughters was not available for all data sets, total number of daughters has been used instead.

Genetic correlations were estimated using an approximate EM-REML procedure, which was tested on simulated and real data, described by Sigurdsson and Banos (1995). The simulation study of Sigurdsson and Banos (1995) indicated the importance of strong ties between countries. Data with no additional information on genetic correlation seemed to disturb the estimation of genetic correlation. In case of weak ties

between countries, but reducing data sets, thus considering only "well connected" data, estimates of genetic correlations were close to the true values. However, direct genetic links, in form of imported proofs, are essential to get good estimates.

In order to provide only strong ties data sets for estimating genetic correlations were reduced to bulls with multiple proofs and full-sib families with members that had proofs in different countries. Besides applying the multivariate model, correlations were also estimated based on bivariate model, including only two different countries.

Evaluations applying MACE with genetic correlation of unity and estimated correlations were run in order to illustrate the impact of genetic correlations on the international ranking of bulls.

3 Results

3.1 Somatic cell count

The heritability used in each country for the national breeding value estimation and estimated sire variances resulting from the de-regression step are shown in Table 3.

Table 3: Trait definition, proof type, heritabilities (h^2) and estimated sire variances (sire σ^2) for somatic cell count Denmark (DNK), Finland (FIN) and USA.

Country	h^2	sire σ^2	Proof type	Trait definition
DNK	0.10	207.4305	AM-SOL [1)]	geometric mean of SCC from period 10-180 days after calving
FIN	0.21	0.0227	AM-SOL	geometric mean of ln of SCC within a lactation
USA	0.10	0.0544	PTA	simple mean of sample day SCS ($=\log_2(SCC/100{,}000)+3$)

[1)] AM-SOL: animal model solutions; PTA: predicted transmitting ability; SCS: somatic cell score.

Table 4 shows the number of bulls with proofs and total number of sires (bulls with proofs and ancestors) included in the data subsets to estimate genetic correlations between countries. Especially connections between Finland and other countries were poor, making good estimation of genetic correlations difficult.

Table 4: Number of bulls and number of sires in data subsets used for estimating genetic correlations for somatic cell counts for multi- and bivariate method.

	Number of bulls	Total number of sires
Multivariate	152	262
Bivariate		
DNK-FIN	19	72
DNK-USA	116	202
FIN-USA	33	86

Table 5 shows the estimated genetic correlations based on the multi- and bivariate method. Genetic correlations estimated by the bivariate method were slightly higher than for the multi-variate method, except for the correlation between Finland and USA. In order to increase the number of bulls, genetic correlation between Finland and USA was also estimated using three-quarter-sibs having proofs in more than one country instead of using only full-sibs. The number of bulls increased to 420 and the total number of sires to 473, the estimated genetic correlation was lower (0.37).

Table 5: Genetic correlations between countries for somatic cell count based on multi- and bivariate method.

	DNK-FIN	DNK-USA	FIN-USA
Multivariate	0.58	0.83	0.55
Bivariate	0.70	0.85	0.56

3.2 Conformation traits

Heritabilities, estimated sire variances and proof type for the 8 conformation traits are shown in Table 6. The number of bulls and sires for the conformation traits data subsets are shown in Table 7. The number of bulls per data subset for the conformation traits was much higher than for somatic cell count, increasing the connectedness of the data, making the estimates for genetic correlations more reliable.

Table 6: Proof type, heritabilities (h^2) and estimated sire variances (σ^2_s) for conformation traits in Canada (CAN), Denmark (DNK) and USA.

Trait	CAN		DNK		USA	
	h^2	σ^2_s	h^2	σ^2_s	h^2	σ^2_s
Stature	0.40	29.64	0.61	7.87	0.42	1.35
Rump	0.30	35.12	0.39	0.69	0.28	1.66
Rump width	0.24	30.02	0.27	0.54	0.26	1.40
Rear leg set	0.16	42.01	0.21	0.53	0.16	2.71
Foot	0.07	40.67	0.21	0.46	0.13	2.38
Fore udder	0.14	37.15	0.23	0.72	0.24	1.84
Central ligament	0.15	30.23	0.15	0.41	0.10	2.89
Teat placement	0.24	31.52	0.36	1.21	0.22	1.96
Proof type	STA[1)]		AM-SOL		PTA	

[1)] STA: standardized transmitting ability; AM-SOL: animal model solutions; PTA: predicted transmitting ability

Table 7: Number of bulls and number of sires in data sets used for estimating genetic correlations for conformation traits for multi- and bivariate method.

Method	Number of bulls	Total number of sires
Multivariate	1339	1665
Bivariate		
CAN-DNK	72	141
CAN-USA	1294	1620
DNK-USA	107	180

The estimated genetic correlations for the eight linear scored conformation traits, based on the bivariate method, and the difference between the bi- and multivariate method are in Table 8. For the small data sets (CAN-DNK and DNK-USA) leaving out redundant data gave increased genetic correlations. Difference in methods for CAN-DNK ranged between +0.02 and -0.20, and for DNK-USA between -0.07 and -0.14. Genetic correlations between CAN and USA were equal for both methods.

Genetic correlations based on the bivariate method were used for a MACE-evaluation for the three countries. Correlations between international and national proofs were 0.99 for all traits for USA, but lower for CAN and especially DNK (Table 9). The lowest correlations for foot angle might probably be related to the low

Table 8: Genetic correlations between countries for conformation traits based on bivariate method; between bracket difference between estimates based on multi- and bivariate method.

Trait	CAN-DNK		CAN-USA		DNK-USA	
Stature	0.83	(-0.08)	0.95	(0.00)	0.84	(-0.10)
Rump	0.88	(-0.11)	0.92	(0.00)	0.91	(-0.11)
Rump width	0.90	(-0.20)	0.87	(-0.01)	0.84	(-0.14)
Rear leg set	0.84	(-0.17)	0.94	(0.00)	0.79	(-0.11)
Foot	0.64	(-0.14)	0.84	(0.00)	0.55	(-0.08)
Fore udder	0.78	(-0.07)	0.94	(0.00)	0.86	(-0.14)
Central ligament	0.79	(-0.12)	0.93	(0.00)	0.86	(-0.17)
Teat placement	0.77	(0.02)	0.95	(0.00)	0.83	(-0.07)

Table 9: Product moment correlation between international and national proofs for all three countries; international proofs based on bivariate estimated genetic correlations.

Trait	CAN	DNK	USA
Stature	0.950	0.961	0.999
Rump	0.976	0.976	0.999
Rump width	0.970	0.958	0.999
Rear leg set	0.971	0.939	0.998
Foot	0.879	0.794	0.998
Fore udder	0.953	0.915	0.999
Central ligament	0.964	0.952	0.996
Teat placement	0.967	0.973	0.998

genetic correlation between countries for that trait. However, this did not affect the correlation between national and international proofs for USA.

To show the impact of genetic correlations less than unity on the ranking of sires within countries, an additional evaluation with genetic correlations of unity was run. Product moment and rank correlation between international proofs based on genetic correlations of unity and bivariate estimates were above 0.95, except for foot in CAN. Table 10 shows the number of bulls in the top 100 for USA that also ranked in the top 100 for CAN and DNK for both methods. It turned out that due to a genetic

correlation less than unity ranking of sires is different in different countries: when using genetic correlation of unity more sires rank in the top 100 in all three countries than using estimated genetic correlations. Traits with lowest genetic correlations showed largest difference in rankings. North American bulls without proofs in DNK got high international proofs in DNK, due to high assumed genetic correlation. Using estimated genetic correlations in the international evaluation international proofs of those bulls were much lower, and more local bulls ranked in the top. The difference for CAN was much lower as most of those North American bulls had a national proof in CAN as well.

Table 10: Number of top 100 bulls in USA which also rank in top 100 in Canada (CAN) and Denmark (DNK) for conformation trait, for genetic correlation of unity and estimated correlation.

Trait	Genetic correlation	Number of USA top 100 bulls with ranking < 100 in:	
		CAN	DNK
Stature	unity	87	87
	estimated	83	54
Rump angle	unity	89	94
	estimated	64	80
Rump width	unity	77	91
	estimated	75	75
Rear leg set	unity	89	92
	estimated	74	60
Foot angle	unity	80	94
	estimated	43	16
Fore udder	unity	89	94
	estimated	75	82
Central ligament	unity	76	86
	estimated	58	60
Teat placement	unity	91	96
	estimated	80	67

4 Discussion and Conclusions

Aim of this study was to estimate genetic correlations for somatic cell count and linear scored conformation traits, using the MACE procedure. For somatic cell count, the data sets were quite small, especially for Finland, leading to weak ties between countries. Genetic correlation was expected to be almost the same level as for production traits because somatic cell count is recorded similar in all countries and preferential treatment seems hard to achieve. However, estimated genetic correlations for somatic cell count were lower than those for production traits, which are about 0.90. Moreover, MACE estimates of genetic correlations compared with proof correlations for bulls with multiple proofs showed much lower MACE estimates (results not shown). This can probably be explained by weak ties between countries, leading to an underestimation of the correlations, which is also shown in the simulation study of Sigurdsson and Banos (1995).

Data sets for conformation traits were much larger, especially for Canada and USA, making reliable estimation possible. Also for the linear scored conformation traits high correlations were expected, since scoring of those traits was harmonized between countries (Cnossen *et al.*, 1993). Estimates of correlations between Canada and USA for both methods were equal for all traits. For correlations between Denmark and Canada resp. USA leaving out redundant information gave increased estimates. MACE estimates agreed fairly good with proof correlations for bulls with multiple proofs.

Table 9 shows the correlations between national and international proofs. The expectation of those correlations is almost unity, as de-regressed proof are regressed in MACE with the same factor used in the de-regression (i.e. reciprocal of total number of daughters). The low correlation for foot might be caused by low heritabilities and genetic correlations. More investigation on these topics is necessary in order to fulfil the expectation the MACE would be applicable to (conformation) traits that are not measured or scored in the same manner in each country, as proposed by Schaeffer (1994).

Data used in this study were animal model solutions (Denmark and Finland) and proofs (Canada and USA) resulting from evaluations performed in each country. Data was not validated for genetic trend. Some studies have already reported discrepancies among estimates of genetic trend (e.g. Banos *et al.*, 1992; Bonaiti *et al.* 1993). Such bias would probably have little effect on efficiency of selection within a country

because candidates for selection are almost contemporary animals. However, the bias provides a distorted picture of the real situation and strongly disturbs international germplasm exchanges based on conversion formulas generally derived from results in different countries for animals of different ages. Boichard *et al.* (1995) described three methods to validate the genetic trend, of which one does not require access to raw data but only to successive official evaluations, and, thus, is applicable by anyone. Because former evaluations were not available the genetic trend was not validated in this research. Results of this study should be interpreted carefully, especially since recent developments showed the weakness of the Canadian type evaluation. Before publication of international evaluations for non-production traits, genetic trend should be validated.

Data used for the estimation of genetic evaluation included both proofs in country of first sampling and imported proofs. Several studies (e.g. Banos *et al.*, 1993a; Banos *et al.*, 1993b) showed biases in genetic evaluation through using imported proofs, which was explained by preferential treatment of daughters of imported bulls. Until recently the genetic evaluation in the USA overestimated the genetic trend, and, thus, overestimated proofs based on second crop daughters. Because the majority of imported bulls are proven bulls from the USA the bias resulting from including imported proofs can be explained by the overestimation of the genetic trend in USA. Besides, considering heterogeneity of variance in the genetic evaluation of the USA might account for some of the effects of preferential treatment.

Sigurdsson and Banos (1995) simulated two dairy cattle populations considering 10 generations, allowing systematic exchange of bulls between countries resulting in well connected populations. One alternative included introduction of bias by multiplying the estimated breeding values of exchanged bulls in the importing country. Results of showed seemingly unbiased estimates of genetic correlation between countries, compared to the true genetic correlation. In the same study the effect of excluding imported proofs was also shown. Using only proofs in countries of first registration showed underestimation of genetic correlation, probably due to weak connections. It was concluded that connections appeared to be the key factor in estimating correlations while biased proofs do not have such a large impact.

Oosterhof (1995) also tested the suitability of MACE to estimate genetic correlations between countries, by simulating data for three different countries and applying Schaeffer's MACE programs to that data. Only proofs in country in first sampling were included, and only exchange sires of sires and dams of sires occurred. Although different genetic correlation were assumed in the simulation, all MACE

estimates of genetic correlation were about 0.95. Differences in degree of exchange did not affect estimates. If unproven bulls were tested in all countries estimates were closer to the true genetic correlation, but were still overestimated. These results might probably be explained by weak connections due to excluding imported proofs, which might affect estimates to a large extent, as shown by Sigurdsson and Banos (1995). However, in their case large underestimation was observed. Moreover, Oosterhof (1995) used all data to estimate genetic correlation and there seems to be a point where the data seems becomes disproportional, i.e. very few direct ties compared to the whole data (Sigurdsson, personal communication). This effect probably also appeared in this study by estimating genetic correlation for somatic cell count by using data of three quarter sibs. Estimates where much lower than those obtained by the "full-sib method" (0.56 vs 0.37).

Because bulls may have various registration numbers in different countries, a cross reference list is used to identify the bull uniquely, utilizing information as best as possible. The same problem exists for cows as well, although import of sires has been more important than import of cows. But because of application of MOET and implementing MOET programs exchange of cows will become more important. It is recommendable to create a cross reference list for cows as well, improving ties between countries, especially in case of estimation of genetic correlations according to the (full-sib) method used in this study. Furthermore, using a cross reference list for cows will give better completeness of pedigrees, which affects estimation of both genetic correlations and international breeding values.

In their discussion about application of genetic groups in an animal model Westell *et al.* (1988) mentioned that group effects can be thought of as accounting for selection not accounted for by records of relatives. They suggested to define groups only for phantom parents that do not have a record, assuming that the phantom parents are average representatives of the genetic groups of similar animals selected to be parents at the same time. The importance of this assumption was demonstrated in the de-regression step by comparing a rough and refined phantom parent grouping strategy, resulting in estimated sire and error variances that were about a factor 2 higher for the rough grouping strategy (results not shown). This also showed the necessity of correctness of birth years, which are not always available for ancestors. Applying three criteria for phantom parent grouping - birth year, selection path and country of origin - number of phantom parents per group will be low in some cases, in

this study for Denmark and Finland, due to small data sets and considerable exchange of semen, giving many different countries of origin. As genetic groups account for differences in genetic merit caused by selection, grouping based on expected genetic merit based on progeny's performance might be considered, equivalent to the strategy applied by Golden *et al.* (1994). More detailed research is needed to study the impact of grouping strategy on (international) evaluations.

As the number of effective daughters which a bull's proof was based on was not available, the total number of daughters was used in both the de-regression step and the evaluation procedure. This will especially affect proofs in country of first sampling based on first crop daughters and imported proofs, as both 'types' of sires will probably have relative low number of daughters per herd. This causes a smaller de-regression of proofs of those bulls and bias in the within country estimates of variances (lower estimates). Estimates of genetic correlations will probably be affected as well, but predicting the direction is difficult.

Genetic correlation less than unity might indicate the existence of genotype by environment interaction. Using estimated genetic correlations in the MACE procedure will favour bulls with proofs in the country for which the international proofs are estimated. Table 10 showed the difference in rankings of bulls between countries, that leads to a bigger active breeding population, and, thus, to a better conservation of genetic variance. Banos and Smith (1991) showed that across country selection (combined selection) of bulls can give considerable increase in genetic response in both countries. Compared to within country selection, increase in genetic response with combined selection was higher when the second country had a higher genetic level and a largere breeding population and if genetic correlation between breeding goals was high. However, genetic correlations between recorded traits less than unity will give a smaller benefit in genetic response.

Results of this study gave reliable estimates for genetic correlations for conformation traits between CAN and USA. Estimates for other countries and for somatic cell count could be underestimated due to lack of connections between countries. More research is necessary to determine the minimum connectedness necessary for estimation of genetic correlations. Moreover, robustness of the method should be tested as well, especially in cases of low heritabilities and genetic correlations.

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Appendix: Description of conformation traits

Interbull trait	CAN	DNK	USA
Stature	Stature	Stature	Stature
Rump	Pin setting	Rump angle	Rump angle
Rump width	Pin width	Rump width	Rump width
Rear leg set	Set of rear legs	Rear legs, side view	Rear leg set
Feet	Foot	Foot angle	Foot angle
Fore udder	Fore attachment	Fore udder attachment	Fore udder attachment
Central ligament	Median suspensory ligament	Udder support	Udder cleft
Teat placement	Teat placement	Front teat placement	Teat placement