

GENOTYPE BY ENVIRONMENT INTERACTIONS IN INTERNATIONAL GENETIC EVALUATIONS OF DAIRY BULLS

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SUMMARY

For international genetic dairy evaluations different environments have been defined as country borders and the genetic component has been progeny tested bulls. The correlations estimated between the countries are affected by differences in trait definition, differences in genetic evaluation model and genotype-environment interactions. Also, genetic correlations estimated between countries can be affected by the amount of exchange of semen expressed as genetic links between the countries. Seven different trait groups and of these 38 different sub-traits are currently evaluated internationally for six dairy breed types. In order to describe the complex of genotype by environment interactions in international genetic evaluations this paper will deal with three of the sub-traits: protein yield, longevity, female fertility (lactating cows' ability to conceive) for the Holstein breed with respect to average correlations, genetic links and model differences between countries that currently subscribe to the international genetic evaluation services for these traits. These three sub-traits were picked to represent 1) *Yield*: a long history of data collection, trait harmonization and genetic evaluation; 2) *Longevity*: a change in trait definition over time due to change in main culling reasons; 3) *Female fertility*: a complex and novel trait in international genetic evaluations. Based on the traits considered in this study it can be indicated that correlations among countries are highest for a trait with a long history of harmonization, and lower for a trait with change in trait definition over time and for a novel trait.

Most countries currently participating in the evaluations have certain environmental similarities. Countries without a national genetic evaluation are buying semen from these countries through semen vendors but breeding values of these bulls are based on progeny tests in totally different environments. Different studies have been looking at inclusion of descriptive variables in order for these countries to get a sire ranking probably more suitable for their environment. The results look promising but are not yet implemented for routine use.

INTRODUCTION

Increased worldwide trade in dairy bull semen in the last 2-3 decades has resulted in a demand for international comparison of bulls from other countries on each country's own scale. For this reason, accurate genetic evaluation of bulls on an international basis requires correct sire rankings for all environments. Differences between sires in the genetic ability of their daughters to perform in different environments may result from true interactions between genotype and environment (GxE). However, performance in neighboring countries with similar production environments cannot be treated as genetically identical traits, due to possible genotype x environment interactions between countries caused by different definitions of the traits or different evaluation models (Fikse *et al.* 2003).

National evaluation bulls' proofs from all member countries are processed together by **Interbull** (International Bull Evaluation Service) and international breeding values are returned to each country on its own scale. The Interbull evaluations started in 1994 with four countries, one breed and three sub-traits. The Interbull evaluation currently (2009) includes 28 countries, 6 breeds and 38 different sub-traits. The numbers of bulls getting an international proof for production traits (the trait group with the largest participation) were in January 2009: Brown Swiss (BSW) 7,922

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bulls; Guernsey (GUE) 944; Holstein (HOL) 105,904; Jersey (JER) 8,692; Red Dairy Cattle (RDC) 11,643; and Simmental (SIM) 22,275.

Globally, dairy selection was for several decades almost solely on production traits. However, due to the negative correlations between production and many functional traits, one-sided selection for production has proven to have a detrimental effect on functional traits (Philipsson and Lindhé, 2003). Functional traits were therefore one after the other included in the national breeding objectives of many countries. This resulted in a demand to have the same traits evaluated internationally as were included in many national genetic evaluations.

The first objective of this paper is to present evidence for GxE for traits of three different types: protein, longevity and female fertility, as examples of traits currently evaluated internationally and the practical implications for the member countries and the industry when ranking the bulls. The second objective is to indicate a method by which countries currently not participating in the international genetic evaluation could benefit from utilizing the information on the different country scales.

COUNTRIES CURRENTLY PARTICIPATING IN THE INTERNATIONAL GENETIC EVALUATION

The aim of international genetic evaluations is to compute international breeding values for all bulls with data sent by countries participating in the evaluations and to deliver back predicted breeding values of bulls from all the countries to each individual country scale.

The process of international genetic evaluations can be divided into two steps. *Step 1* deregression (Jairath *et al.*, 1998) and estimation of genetic correlations among countries (Klei and Weigel 1998) and *step 2* deregression, sire variance estimation (Sullivan 1999) and prediction of international breeding values. Steps 1 + 2 are done twice per year during the “Test Evaluations” where new countries or new traits or new breeds can join the evaluations, while step 2 only is performed for the three yearly “Routine Evaluations”.

Multi-trait Across Country Evaluation (MACE) software (Klei, 1998; Klei and Weigel 1998) is used to obtain the genetic correlations. Genetic correlations among countries are post-processed using prior information about previously estimated correlations, national production systems and trait definitions. These post-processed correlations are used for prediction of breeding values across countries. The average correlations per country for protein yield, longevity and female fertility are shown in Tables 1, 2 and 3, respectively, for the Holstein breed. The tables also show how far back each country includes data for these traits in their national genetic evaluation, the trait definition, their national genetic evaluation model, heritability of the trait as well as average number of common bulls. Apart from the average number of common bulls and average genetic correlations all the information in these three tables is provided by the Interbull member countries in the so called GE-forms where they describe the national genetic evaluation system for each specific trait group (Interbull 2009).

Tables 1 to 3 show that average correlations are the highest for production traits, with a mean of 0.84, and medium for both female fertility (0.63) and longevity (0.66). The history of milk recording is much longer than the collection of information about culling and fertility, and production traits have therefore had a greater opportunity to reach a higher degree of trait and model harmonization than the other traits.

Longevity is a trait that is very difficult to harmonize partly because the time of culling may be determined by agricultural policy or product price changes in a country. This may easily cause the main culling reasons to change over time. A survey sent to the Interbull community (Forabosco *et al.* 2009) on the main culling reasons showed that poor female fertility is the main reason for culling today in most of the member countries. However, some countries do not collect the information about culling reasons at the national level. It can only be speculated what the

responses would have been if the survey had been conducted 15-20 years ago, when more cows may have been culled due to low production. Tarres *et al.* (2007) estimated genetic correlations between longevity in Germany and longevity in France using different left censoring for data inclusion. They found that correlations between these two countries for longevity changed from 0.694 to 0.731 to 0.845 when 1985, 1990 and 1995, respectively, were used for left censoring of data. This indicates a change of the longevity trait definition over time for the countries included in their analysis. A change in trait definition over time for productive life in the US was confirmed by Tsuruta *et al.* (2004). Some countries have productive longevity as their official trait while others have functional longevity. The Netherlands changed their trait definition from functional longevity to productive life in 2008 and noticed an average decrease in genetic correlations to other countries of -0.18 (Van der Linde and de Jong 2007), where the decrease was largest to countries having functional longevity. This indicates that a change in trait definition can change correlations to other countries and that the similarity in trait definition among countries will affect the correlation.

Currently, International genetic evaluations for female fertility are offered for five different sub-trait groups: *T1*: Maiden heifers' ability to conceive; *T2*: Lactating cows' ability to recycle after calving; *T3*: Lactating cows' ability to conceive expressed as a rate trait; *T4*: Lactating cows' ability to conceive expressed as an interval trait (all countries are expected to submit a trait for this trait group and can even submit a rate trait for this sub-trait); *T5*: Lactating cows' measurements of the interval traits calving-conception. In this study we looked at sub-trait group *T4* because it includes all countries, but the differences in trait definition impacted the average genetic correlation reported for female fertility. Computing the average correlation for a pure rate trait as *T3* gave a correlation of 0.71 and slightly higher than the average for the *T4* sub-trait group.

National evaluation models used to analyze protein, longevity and female fertility are also shown in Tables 1 to 3. Emanuelson *et al.* (1999) showed that changes in national genetic evaluation models can impact correlations to other countries in both directions depending on the nature of the model change.

The size of the correlations among countries affects re-ranking of bulls on other country scales. If the genetic correlations are unity the ranking of the bulls will be the same on all country scales, but as soon as the correlation is smaller than one some re-ranking will occur. In general, the smaller the correlation, the more re-ranking of bulls. Figure 1 illustrates the number of bulls appearing on a top 100 list for protein and longevity in any participating country for each of the evaluations from February 2006 to January 2009. If the correlation had been one, the same 100 bulls would have been selected for any country, but as the correlations are less than unity the figure shows that 362 and 655 bulls appeared on a top 100 list for one of the countries participating in the January 2009 evaluation for protein and longevity, respectively.

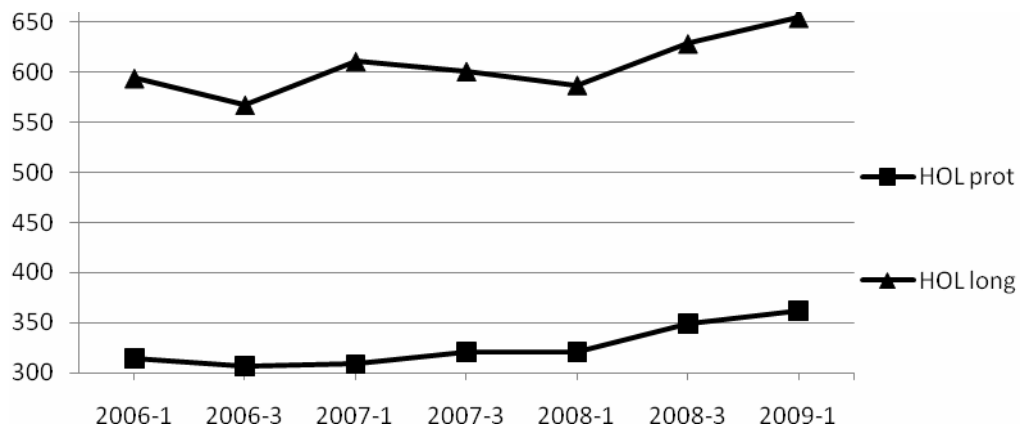


Figure 1. Trend of the total number of top 100 Holstein (HOL) bulls for protein (prot) and longevity (long) traits when $r_g < 1$.

Average number of common bulls for each of the countries participating in the evaluations for production, longevity and female fertility are also shown in Tables 1 to 3. Good links to other countries are required for estimation of reliable correlations. Semen of the Holstein breed has been distributed over large parts of the world and for most populations links are rather strong. The average number of common bulls ranged from 31 (Israel) to 472 (United States) for protein, from 8 (Denmark – Red HOL) to 476 (United States) for longevity and from 44 (Israel) to 762 (United States) for female fertility. Average number of common bulls for individual countries cannot be compared across traits as the value is influenced by which countries are participating in the evaluation, how much semen exchange there has been among these countries, how well the international animal identification is harmonized and also the novelty of the trait in respect of national evaluations. Large populations have by definition a larger chance of having large number of common bulls than small populations. However, the issue is also what proportion of tested bulls are used in common with other countries.

COUNTRIES CURRENTLY NOT PARTICIPATING IN THE INTERNATIONAL GENETIC EVALUATION

Many countries around the world may for political, economical or infrastructural reasons not have a national genetic evaluation in place and neither an organized animal identification nor a milk recording system. With that in mind there is no opportunity of joining the international genetic evaluation for dairy bulls in the near future. However, semen from other countries is sold in these countries but bulls' breeding values cannot be presented on a country scale of the purchasing country. Bulls may have been progeny tested in a temperate environment with one sort of management system (e.g. lots of concentrate feeding and/or low fibre grass diet) and sold to a tropical environment with a different management system (e.g. very limited concentrate feeding and/or high fibre grass diet) and daughter performance of these bulls may be very different in these environments. This is confirmed by, among others, Ojango and Pollot (2002) who found a genetic correlation between breeding values of bulls tested in both the UK and Kenya of 0.49.

Also, environmental factors, such as temperature and humidity, may differ a lot between the different environments. G x E exists within large countries such as the United States and therefore Weigel *et al.* (2001) and Bohmanova *et al.* (2008) suggested including effects of temperature and humidity in the US national genetic evaluation model for milk production in order to account for the heat stress / heat tolerance factor in the model.

It would be very desirable for the importing non-Interbull member countries to have a tool that can be used when selecting bulls that would perform the best under their environmental conditions.

Mark *et al.* (2006) and Torsell *et al.* (2007) worked on procedures to produce a good estimate of a correlation between the countries currently participating in the Interbull evaluations and non-participating countries. Torsell *et al.* (2007) applied the currently used REML procedure (Sigurdsson *et al.* 1996) to several different scenarios without inclusion of data from a pilot country and compared the results of the different scenarios to the results obtained using data from a pilot country. Among the scenarios tested was the use of different fixed correlations between the country with no data and all other countries but also inclusion of different environmental descriptors as climatic variables, production system indicators and information about national genetic evaluation systems in their model. They found that the scenario including environmental descriptors gave a better result than the scenarios using fixed correlations.

These procedures are not yet implemented for routine use, but show the opportunities for countries not participating in Interbull evaluations to benefit from the international genetic evaluation system. In order to get that system to be operational it is necessary to include relevant environmental descriptors for all countries participating in Interbull evaluations as well as for those countries wanting to participate without own data. Selection of breeding animals using genomic selection will have an impact on selection of the dairy breeds also in these countries, yet the G x E among countries need to be considered as apparently different environments require different animals. The issue is to get as good estimates as possible of the genetic correlations, even when national evaluation systems are lacking.

CONCLUSION

Genetic correlations less than one exist among the countries currently enrolled in the Interbull evaluation and are affected by trait definition, national genetic evaluation model, and G x E interactions. Three of the thirty-eight sub-traits currently evaluated were described in this paper to represent different dimensions of the genetic by environment interaction complex for international genetic evaluations. Currently, environments are separated by national country borders, due to the fact that most genetic evaluation units are national, but could theoretically be defined by other environmental descriptors. Many non-Interbull member countries import semen from bulls tested in a different environment and daughters of these bulls seem to perform differently in the local environment indicating G x E interactions. These countries may not be able to participate in the International evaluation with their own data but may be able to convert breeding values from other countries to their own scale including predefined environmental descriptors as prior information.

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Table 1. Country (COU), first year of data inclusion for current national genetic evaluation, trait definition, genetic evaluation model, heritability (h^2), average number of common bulls (μ_{CB}) and average post-processed correlations to other countries (μ_{RG}) for international genetic evaluation for protein yield for the Holstein breed in April 2009.

COU ¹	Data since	Trait definition ²	Model ³	h^2	μ_{CB}	μ_{RG}
AUS	1975	305 d yield; complete and extended lactations	ST RP AM	0.250	246	0.77
BEL	1973	Yield within a 24 hour test period; EBV: average 305 day yield across Lact. 1-3	MT ML RR TD AM	0.410	164	0.84
CAN	1988	Yield within a 24 hour test period; proofs are average yields across Lact. 1-3	MT ML RR TD AM	0.370	308	0.86
CHE	1985	Test day yield. Lact 1-3; records < 330 DIM	MT ML RR TD AM	0.320	134	0.86
CHR	1987	Test day yield. Lact 1-3; records 5-330 DIM	MT ML RR TD AM	0.360	123	0.86
CZE	1995	Yield within a 24 hour test period; Lact 1-3.	ST ML RR TD AM	0.370	295	0.84
DEU	1990	Yield within a 24 hour daily basis; Lact. 1-3. Records 5-330 DIM	ST ML RR TD AM	0.480	448	0.84
DFS	1990(DNK),1988(FIN), 1995(SWE)	Test day yield (DNK+FIN), lactation records (SWE), Lact 1-3 (DNK+SWE), all lactations (FIN)	MT ML RR TD AM	0.390	293	0.86
ESP	1986	305 d yield; complete and extended lactations; Lact 1-5	ST RP AM	0.280	230	0.85
EST	1994	Test day yields 5-365 DIM. Lact 1-3.	ST ML RR TD AM	0.480	41	0.86
FRA	1980	305 d yield; complete and extended lactations; Lact 1-3	ST RP AM	0.300	253	0.86
FRR	1980	305 d yield; complete and extended lactations; Lact 1-3	ST RP AM	0.300	10	0.86
GBR	1975	Test day yields. Lact 1-5	ST ML RR TD AM	0.510	359	0.85
HUN	1985	305 day yield. Lact 1-3	ST RP AM	0.200	232	0.85
IRL	1970	305 day yield. Lact 1-5	ST RP AM	0.350	174	0.78
ISR	1985	305 day yield; complete and extended lactations	ST ML AM	0.410	31	0.78
ITA	1985	Test day yield within 24 hour period. Lact 1-3; records 5-305 DIM	MT ML RR TD AM	0.300	298	0.85
JPN	1985	305 day yield; Lact 1-5.	ST RP AM	0.270	113	0.87
LVA	1996	Yield within a 24 hour test period. Lact 1-3.	ST ML RR TD AM	0.480	36	0.85
NLD	1990(NLD), 1981(FLA), 1995(LUX)	Yield within a 24 hour test period. Lact 1-3. Records 5-335 DIM.	ST ML RR TD AM	0.500	446	0.85

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Table 1 continued. Country (COU), first year of data inclusion for current national genetic evaluation, trait definition, genetic evaluation model, heritability (h^2), average number of common bulls (μ_{CB}) and average post-processed correlations to other countries (μ_{RG}) for international genetic evaluation for protein yield for the Holstein breed in April 2009.

COU ¹	Data since	Trait definition ²	Model ³	h^2	μ_{CB}	μ_{RG}
NZL	1986	Test day records 3-270 DIM. Age groups 2, 3, 4, and 5-7 years	ST ML RR TD AM	0.310	234	0.76
POL	1995	Test day records 5-305 DIM. Lact 1-3.	ST ML RR TD AM	0.290	216	0.84
SVK	1992	Yield within a 24 hour test period. Records 5-365 DIM. Lact 1-3.	ST RR TD AM	0.300	102	0.85
SVN	1997	Test day records 6-305 DIM. Lact. 1-5.	ST RP FR TD AM	0.210	38	0.85
USA	1960	305 day yield; complete and extended lactations. Lact 1-5	ST RP AM	0.300	472	0.86
ZAF	1988	Yield within 24 hour test period. Records: 5-305 DIM. Lact 1-3.	MT RP FR TD AM	0.140	174	0.84

1. AUS=Australia; BEL=Belgium, CAN=Canada, CHE=Switzerland (black & white), CHR=Switzerland (red&white), CZE=Czech Republic, DEU=Germany, DFS=Denmark+Finland+Sweden, ESP=Spain, EST=Estonia, FRA=France, FRR=France (red&white),GBR=United Kingdom, HUN=Hungary, IRE=Ireland, ISR=Israel, ITA=Italy, JPN=Japan, LVA=Latvia, NLD=The Netherlands, NZL=New Zealand, POL=Poland, SVK=Slovak Republic, SVN=Slovenia, USA=United States, ZAF=South Africa
3. DIM=Days in milk 3) ST=Single trait, MT=multiple trait, ML=multiple lactations, RR=random regressions, RP=repeatability, FR=fixed regression, AM=animal model, TD=test-day model

Table 2. Country(COU), first year of data inclusion for current national genetic evaluation, trait definition, genetic evaluation model, heritability (h^2), average number of common bulls (μ_{CB}), and average post-processed correlations to other countries (μ_{RG}) for longevity evaluation for the Holstein breed in April 2009.

COU ¹	Data since	Trait definition	Model ²	h^2	μ_{CB}	μ_{RG}
AUS	1975	Probability of surviving from one year to the next	AM RP	0.025	309	0.61
BEL	1973	Survival over successive lactations	AM RR	0.106	157	0.66
CAN	1980	Survival in the first three lactations	AM MT	0.098	322	0.76
CHE	1980	Productive life span of the cow in months	SM SA	0.077	154	0.75
CHR	1984	Productive life span of the cow in days	SM SA	0.110	88	0.67
DEU	1985	Functional herd life in days	SM SA	0.166	335	0.75
HUN	1988	Productive life span of the cow in days	SM SA	0.050	232	0.51
DNK	1984	Productive life span of the cow	SM SA	0.117	169	0.74
DNR	1984	Productive life span of the cow	SM SA	0.117	8	0.69
ESP	1986	Productive life span of the cow in days	SM SA	0.115	240	0.66
FIN	1988	Stayability from first calving	SM SA	0.120	49	0.65
FRA	1988	Productive life of the cow in days	SM SA	0.108	260	0.66
NLD	1988	Productive life span of the cow in days	SM SA	0.120	377	0.61
NZL	1987	Survival from first to fifth lactation	AM MT	0.055	256	0.48
GBR	1986	Lifespan	AM MT	0.064	442	0.75
IRL	1980	Survival to the next lactation (lactation 1 to 4)	AM MT	0.016	221	0.71
ISR	1985	Days from first calving to 2922d.	AM ST	0.110	34	0.57
ITA	1980	Productive life span of the cow in days	SM SA	0.097	307	0.61
SWE	1984	Survival rate at second calving	SM MT	0.080	230	0.65
USA	1960	Productive life	AM ST	0.080	476	0.76

1) AUS=Australia; BEL=Belgium, CAN=Canada, CHE=Switzerland (black & white), CHR=Switzerland (red&white), DEU=Germany, HUN=Hungary, DNK=Denmark (black&white), DNR=Denmark (red&white), ESP=Spain, FIN=Finland, FRA=France, NLD=The Netherlands, NZL=New Zealand, GBR=United Kingdom, IRL=Ireland, ISR=Israel, ITA=Italy, SWE=Sweden, USA=United States

2) AM=animal model, SM=sire model, ST=single trait, MT=multiple trait, SA=survival analysis

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Table 3. Country (COU), first year of data inclusion for current national genetic evaluation, trait definition, genetic evaluation model, heritability (h^2), average number of common bulls (μ_{CB}), and average post-processed correlation to other countries (μ_{RG}) for female fertility (lactating cows ability to conceive) evaluation for the Holstein breed in April 2009.

COU ¹	Data since	Trait definition	Model ²	h^2	μ_{CB}	μ_{RG}
BEL	1980	Pregnancy Rate	ST AM	0.040	463	0.68
CAN	1996	Interval first insemination-conception in cows	MT AM	0.077	292	0.70
CHE	1994	Non return rate after 56 days	MT AM	0.010	277	0.43
CHR	1994	Cows' non return rate after 56 days	MT AM	0.010	186	0.46
CZE	1993	Cows' conception rate (pregnant or not after 3 months)	SM GSM	0.030	226	0.63
DEU	1995	Interval from first to last insemination cows	MT ML RP AM	0.010	714	0.74
DFS	1990(DNK),1988(FIN),1995(SWE)	Interval from first to last insemination cows (days)	SM RP	0.020	461	0.73
ESP	1986	Days open	ST RP AM	0.045	686	0.72
FRA	1995	Cows' conception rate (binary trait) for cows	MT AM	0.020	582	0.65
GBR	1992	Days between 1st and 2nd calving	MT AM	0.033	632	0.65
IRL	1980	Calving interval	MT AM	0.037	405	0.65
ISR	1985	Inverse of the number of insemination to conception	MT AM	0.067	44	0.52
ITA	1990	Calving Interval (days)	MT AM	0.038	512	0.69
NLD	1978(NLD), 1975(FLA)	Calving Interval	MT AM	0.145	704	0.65
NZL	1990	Lactating cow's ability to conceive	MT ML AM	0.030	354	0.49
USA	1960	Daughter pregnancy rate	ST RP AM	0.040	762	0.75

1) BEL=Belgium, CAN=Canada, CHE=Switzerland (black & white), CHR=Switzerland (red&white), CZE=Czech Republic, DEU=Germany, DFS=Denmark+Finland+Sweden, ESP=Spain, FRA=France, GBR=United Kingdom, IRL=Ireland, ISR=Israel, ITA=Italy, NLD=The Netherlands, NZL=New Zealand, USA=United States

2) ST=Single trait, MT=multiple trait, ML=multiple lactations, RP=repeatability, AM=animal model, SM=sire model