

International genetic evaluation of dairy cattle

Georgios Banos
INTERBULL Centre
Department of Animal Breeding and Genetics
Swedish University of Agricultural Sciences
750 07 Uppsala, Sweden

SUMMARY

International genetic evaluation of dairy cattle can provide valuable selection tools to dairy producers around the world. The demand for such development has grown as international exchange of genetic material has been rapidly increasing. Several factors affecting the success of a global evaluation system are discussed in this article. Alternative methods are described and assessed. Their relative merits depend on two inversely proportional components: simplicity of implementation and accuracy of results. The method that currently combines best these two attributes is computation of a single international proof following linear model analysis of national evaluations of bulls across country. Extensive research experience regarding this method has been gained, showing its feasibility for large scale applications. Further research is planned to determine the complete global evaluation system of the future which should effectively cover the maximum number of populations, environments, and breeding goals.

INTRODUCTION

Intensification of dairy cattle breeding continues as the turn of the century approaches. At the same time, borders throughout the world open, international co-operation is pursued more and more eagerly, and it becomes clear that the winners of the future will be those who will most efficiently exploit this globalization.

The merits of sensible internationalization of dairy cattle breeding have been theoretically documented (Banos and Smith, 1991; Goddard, 1992). In practice, examples of rapid progress can be found in countries which looked beyond their borders to find the best genetics (Burnside et al, 1992).

Intensification and globalization of dairy cattle breeding does not necessarily imply complete domination of one major breed (Holstein-Friesian) and simultaneous elimination of smaller breeds. In the latter, individual country populations can also become competitive in the international scene by effectively pooling resources (Philipsson et al, 1992).

Today's breeders must be able to select the best genetics from anywhere in the world in order to meet the challenge and stay competitive. Identifying the best breeding animals regardless of their national origin is the first step towards successful selection. This requires some sort of simultaneous genetic evaluation of all potential candidates across country.

At present, each country genetically evaluates animals from its own population as well as animals imported. Thanks to a series of statistical and computational advances, these national evaluation procedures have reached high levels of sophistication and have found large scale applications (Jansen, 1990), but still provide only within country selection tools. Philipsson (1987) gave a full account of the reasons preventing genetic evaluations from different countries to be directly compared.

Knowledge of the genetic differences between cattle populations is usually lacking although required in international genetic comparisons. Experimental studies have been undertaken to evaluate average relative genetic merits of various stocks (Hinkovski et al, 1979; Stolzman et al, 1981). Periodic repetition of such carefully designed experiments together with close monitoring of the genetic progress observed in each country could result in meaningful international comparisons. Alternatively, genetic differences among populations could be computed simultaneously with international genetic evaluations of individual animals, in a more continuous process parallel to within country evaluation procedures.

In this article, the concept of international genetic evaluations of individual animals rather than strains or populations is addressed. Methods for global genetic evaluations are described, the current "know-how" is reviewed and assessed, and the potential for future improvement is discussed.

GENERAL CONSIDERATIONS

Several factors determine the feasibility of global genetic evaluations of dairy cattle and are synopsized next. The effect of these factors on specific global evaluation methods is discussed in the following chapter.

Data availability

The amount and quality of data provided by each country depend on a host of components starting from the recording philosophy and ending with the national genetic evaluations. The number and definition of traits recorded depend on tradition, the infrastructure of the national dairy industry as a whole, technical advances, and the definition of the breeding goal. These components usually vary across country as well as across breed within a country.

Data connectedness

Provided that usable records become available from several countries, the next consideration is that data are well connected across country. Existence of genetic links among corresponding cattle populations would provide connectedness of the combined data. Such links can be developed directly via importations and exportations or indirectly via usage of genetically tied animals. Here genetic ties are not necessarily limited to individuals with common ancestry but include individuals with common descendants; for example, a bull's sire and maternal-grand-sire are not genetically related but are tied because of their common relationship to the bull. Banos and Cady (1988) proposed a method to estimate such genetic ties between different bull populations.

In an analysis of disconnected data, linear functions of fixed effects become inestimable and predictions of random effects inaccurate. Several methods have been developed to assess data connectedness in within country genetic evaluations (Petersen, 1978; Fernando et al, 1983; Tosh and Wilton, 1990). Foulley et al (1992) suggested a connectedness index, known as the Kullback-Leibler distance, to measure connectedness between effects in a linear model of genetic evaluation. Kennedy and Trus (1993) considered measures associated with the average prediction error variance of differences in genetic evaluations of animals in different management units as connectedness criteria. The above methods can be conceptually extended to cover genetic evaluations across country.

Ranking under different conditions

The same animals may rank differently under varying conditions (e.g. countries, national evaluation systems, environments etc). Reasons causing such discrepancies are: genuine genotype by environment interaction (GxE) where animals perform differently under various production systems; differences in recording options or trait definition resulting in genetic correlations (r_G) among countries of less than unity; heterogeneity of genetic parameters (genetic variance, heritability) associated with distinct cattle populations. Failing to properly account for these effects will cause inaccurate predictions under some conditions.

Most research studies have shown little evidence of true GxE across country for dairy production traits (Carabaño et al, 1989; Syrstad, 1990; Stanton et al, 1991). Contrary to these observations, Peterson (1991) reported presence of GxE between the Canadian and New Zealand environments and cattle populations.

The genetic correlation between two countries can be less than unity even under the same environmental conditions, if the trait in question is defined differently. This is especially true for subjectively assessed non-dairy-production traits (e.g. calving performance, milkability, conformation, temperament etc). Dairy production traits described by the first and multiple lactations may also have r_G of less than one.

Heterogeneity of genetic parameters across country has been reported by Carabaño et al (1989) and Stanton et al (1991). Under its presence, international evaluation will result in unfair advantages to animals from countries with highest genetic variances.

Mixing populations

When importations take place additional problems may arise. Records associated with imported animals or their immediate relatives (e.g. bull daughters) can be biased due to heterosis and/or preferential treatment. Heterosis arises from breeding genetically different livestock strains and has particular effects on non-dairy-production traits associated with fitness. However, dairy production traits may also be influenced by heterosis (Zarnecki et al, 1993). Preferential treatment refers to imported cows or bull daughters resulted from expensive imported semen enjoying exclusive managerial privileges compared to their herdmates. Possible introduction of the bovine somatotropin in the commercial breeding will accentuate this problem. While heterosis can be properly adjusted for (Van der Werf and de Boer, 1989; Boichard et al, 1993), preferential treatment remains a chronic problem haunting geneticists around the world.

METHODS OF GLOBAL GENETIC EVALUATION

The development of artificial insemination and the extensive exchange of frozen semen across country has prompted the development of methodology to compare bull genetic evaluations (proofs) calculated in different countries. Two such methods are reviewed next.

Additionally, the interest to identify the best female animals regardless of origin, together with an increase in their reproductive potential, have motivated the development of a global genetic evaluation based on raw data (e.g. lactation records). This is an extension of the simultaneous national genetic evaluations of bulls and cows applied in several countries and is also discussed in further detail next.

Comparison of bull proofs from various countries

a) Conversion of national proofs

The most widespread method to compare bull proofs from various countries is to convert proofs from one country (P_A) to figures equivalent to another (P_B) by performing a simple regression (Model 1):

$$P_B = a + b \cdot P_A \quad [1]$$

The coefficients a and b represent the reference base and the scale difference, respectively, between the two countries. The b -value may also include an adjustment for the accuracy of the national proofs and genetic correlation of less than unity between the two countries (Goddard, 1985; Wilmink et al, 1986).

In order to compute the above conversion coefficients, common bulls must be evaluated in the two countries. According to Model 1 these common bulls are either simultaneously tested in the two countries or first tested in country A and then exported to country B. Recommendations on estimation, proper use, and validity of such conversions have been worked out by the International Bull Evaluation Service (INTERBULL, 1990).

Model 1 allows bull proofs from two countries at a time to be compared. When more countries are involved, several pairwise sets of conversions must be computed.

This method has found wide application in many importing countries considering dairy production and conformation traits; it is simple and straightforward to apply and is associated with very low cost. Further, it accounts for genetic correlation of less than unity between countries which promptly accommodates any source of re-ranking due to different conditions.

Prerequisite for applying Model 1 is that direct ties between the two countries exist. In absence of sufficient direct ties a third intermediate country can be considered to compute conversion coefficients indirectly. Such practice, however, may be quite unreliable resulting in substantial errors (Banos, 1993).

A problem associated with conversions is that computations of the a and b coefficients are usually based on a small number of highly selected bulls whose genetic merit in the importing country may be over-predicted, possibly due to preferential treatment of their daughters. Studies conducted at the INTERBULL Centre in Sweden (Banos et al, 1993 and 1994) revealed average upwards bias of imports' proofs reaching 5-6% of the mean for dairy production traits in some European countries. Individual bull proofs were much more severely affected. Using these proofs to compute conversions would lead to inflation of the a -value; bull proofs converted from the exporting country would then be over-predicted by as much as 25%. A possible solution is to consider sire-son regressions, but longer time intervals would be needed before sufficient data could become available. Use of existing full-sib families (Mattalia and Bonaiti, 1993) may provide a more attractive alternative in estimation of conversion coefficients.

b) *Linear model analysis of national proofs*

This method combines national evaluation results from several countries and returns an international BLUP estimate of each bull's genetic merit using linear model analysis. An international evaluation model was suggested by Schaeffer (1985) as follows:

$$y = Xc + ZQg + Zs + e \quad [2]$$

Where

- y: Observations vector;
- c: Country of evaluation fixed effect;
- g: Genetic group of bull fixed effect;
- s: Bull random effect; $\text{Var}=A\sigma^2$, A is the numerator relationship matrix of bulls;
- e: Residual random effect; $\text{Var}=R\sigma^2$, R^{-1} is a diagonal matrix with diagonals associated with the accuracy of each national proof (e.g. number of daughters, effective number of daughters etc);
- X, Z, Q: Incidence matrices.

In Model 2 there is one observation per bull and country of evaluation, representing either Daughter Yield Deviation (VanRaden and Wiggans, 1991) or de-regressed national proof (Banos et al, 1991). These observations are standardized within country using the sire standard deviation (Banos et al, 1993) to account for differences in unit definition and possible heterogeneity of variance across country. Genetic groups may be defined by the bull's birth year, population of origin, breed composition and other factors deemed important in each case.

International evaluations for dairy production traits using variations of Model 2 have been addressed in several research projects: Rozzi et al (1990) jointly evaluated Canadian, Italian, and US Holstein-Friesian bulls, Jacques and Klemetsdal (1990) compared Red-and-White (Ayrshire type) bulls from the Nordic countries, Banos et al (1991) considered Ayrshire and Jersey Canadian and USA bulls, and Banos et al (1993, 1994) evaluated Holstein-Friesian bulls from several European and North American countries.

As explained earlier, prerequisite for an international evaluation with a linear model is that data are well connected across country implying existence of genetic links among corresponding bull populations. The connectedness index suggested by Foulley et al (1992) was considered in some of the above studies to assess connectedness between the country and genetic group effects in Model 2. Estimates ranged from .7 to .8 in the 0 to 1 continuous scale (high values indicate high degree of connectedness). Holstein-Friesians appeared better connected across country than other breeds, reflecting stronger links and wider genetic exchange among various populations. The genetic drift variance among countries based on genetic relationships between and within country (Kennedy and Trus, 1993) was also found substantially reduced due to presence of sire connections. In the cases studied, populations were sufficiently linked to justify joint evaluation with Model 2. These connectedness criteria are now being considered in similar studies of Ayrshire and Guernsey bull populations from Europe, North America, and Oceania.

The major advantage of this method is that all national proofs available can be used, instead of proofs of bulls with evaluations in more than one country as with conversions. Genetic relationships among bulls are used to link information from different sources (countries) and

a single international bull proof is obtained. Also there is no limit to the number of countries considered simultaneously.

An additional advantage is that potentially biased information from the importing countries can be excluded. Banos et al (1993, 1994) showed that it is possible to base an international evaluation only on data from the bulls' country of first sampling as well genetic relationships among bulls.

A disadvantage of Model 2 is that genetic correlations of unity are assumed among countries. Violations of this assumption would result in biased, inaccurate international proofs. A variation of this model that allows genetic correlations among countries to be less than unity has been presented by Schaeffer and Zhang (1993). The revised model calculates separate international proofs for each country. This approach would relax the assumption associated with Model 2 but caution must be exercised in the choice of genetic parameters within and across country.

An additional consideration pertaining to this method is that it is based on results of various national evaluations. Banos et al (1993) in a collaborative study between INTERBULL and the European Union, realized that a major prerequisite for such a linear model analysis is conformity among the national evaluation systems with regards to inclusion and definition of fixed effects and calculation of Daughter Yield Deviations. The former is particularly important since it has direct bearing on the estimation of genetic trend; inconsistencies in this area would result in some countries having an unfair time advantage over others. Bonaiti et al (1993) have suggested a procedure to validate the genetic trend estimation in each country prior to an international evaluation with Model 2. Furthermore, individual national evaluation systems are assumed to have accounted for non-random mating of bulls, selective usage of bulls in high variance herds, and possible heterosis effects.

Experience to date has shown that, under the conditions stated earlier, application of this method for international genetic evaluation is feasible and worthwhile. INTERBULL currently considers routine computation of international genetic evaluations of bulls for dairy production traits across its member-countries. More research is planned to assess the method's suitability for non-dairy-production and beef production traits.

Global genetic evaluation based on individual performance records

Theoretically the most accurate international evaluations would be computed by a joint analysis of raw data (e.g. lactation records, classification scores etc) across country. This can be seen as an extension of within country animal model evaluations. Example evaluations for dairy production traits have considered the Ayrshire and Jersey breeds in the USA and Canada (Powell et al, 1991; Robinson and Wiggans, 1991) and the Holstein-Friesian breed in Italy and Spain (Rozzi et al, 1991), as research projects.

This method is advantageous since it makes use of all possible information. Potentially biased records associated with imported semen can be excluded from the analysis, if deemed necessary. The issue of data connectedness must also be addressed as described earlier. Presence of genotype by environment interaction, heterogeneity of variance across countries, and heterosis effects have to be investigated and, if needed, accounted for in the model of international evaluation.

There are also several problems associated with such an application. Recording options in different countries may limit the amount of available data. Sources of systematic variation may differ substantially from country to country, turning the choice of an appropriate, widely accepted international animal model to a formidable task. Computing requirements may pose a temporary constraint. More experiences with international data exchange must be gained before individual animal performance records are efficiently handled. The suitability of this method for traits other than dairy production has yet to be determined. Eventual possible replacement of individual national evaluations with such a joint international evaluation will require much additional co-operation among countries.

CONCLUDING REMARKS AND FUTURE OUTLOOK

Substantial research and development efforts have been put in deriving proper methodology for international evaluations of dairy cattle. Within current time and computing limitations the most accurate method readily available is computation of a single international bull proof using linear model analysis of national evaluation results from various countries. Extensive experience regarding this method has been gained with several pilot applications on dairy production data. At the same time the international community appears ready to receive this type of results. International proofs computed with this method would complement national evaluations as selection tools.

A variation of this method which allows genetic correlations among countries to be less than unity deserves more research attention. Such application would enhance the capacity of the method and cover many more countries with different production systems.

International evaluations can not be restricted to dairy production traits. A variety of additional important traits related to disease resistance, reproduction, management, conformation, and growth need to be also addressed. Global evaluations must serve all possible breeding goals. Therefore, INTERBULL is currently placing particular emphasis in developing methodology suitable for these traits.

To date the feasibility of global evaluations for Holstein-Friesian, Ayrshire, Jersey, and Guernsey breeds has been addressed in separate research projects. The foundation has been laid for expansion to cover all other dairy and dual purpose breeds of international interest.

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