

PREDICTION OF INTERNATIONAL BREEDING VALUES OF DAIRY SIRE USING INDIVIDUAL ANIMAL PERFORMANCE RECORDS

K. A. Weigel

Department of Dairy Science, University of Wisconsin
1675 Observatory Drive, Madison, WI, 53706, USA

INTRODUCTION

Genetic improvement of dairy cattle has become a global venture. Farmers routinely use semen of foreign sires, and breeding companies acquire genetics from a variety of countries. With the international exchange of cattle, semen, and embryos comes a need for methods to compare animal that differ in housing conditions, feeding programs, and genetic composition of mates. Years ago, when genetic differences between strains of cattle in different countries were large, a simple comparison of phenotypic records sufficed. Over time, however, countries that were once importers of genetic material became competitors, with export aspirations of their own. Genetic differences between countries and strains are smaller, and advanced statistical procedures are needed to compare animals fairly and accurately.

REVIEW OF METHODOLOGY

Regression-Based Conversion Equations. Initial methods to compare dairy sires that were progeny tested in different countries were based on linear regression. Goddard (1985) and Wilmink *et al.* (1986) proposed methods that utilized daughter yield deviations (DYD) and estimated breeding values (EBV) of local progeny, respectively. Parameters of these equations were estimated from bulls that had progeny in both the importing and exporting countries, but this posed several problems. The number of bulls with progeny in both countries was often small, and this limited the accuracy and stability of the resulting equations. Furthermore, new countries could not even obtain conversion equations until they compiled several years of historical data from progeny of imported sires. Finally, because of genetic trend, the merit of new bulls in the exporting country, to which the conversion equations would be applied, was often far higher than any of the older bulls that were used to develop the regression equations. Weigel (1997) noted that the accuracy of converted EBV for elite sires, which were the animals of most interest, was far lower than that of average sires, because the EBV of these sires were outside the range of data that were used to develop the equations. Mattalia and Bonaiti (1993) proposed conversion equations based on data from full brothers in which at least one member of each full-sib family had progeny in both the importing and exporting country, but the number of full-sib families is limited for many pairs of countries.

Extension to a Linear Model. The next major development was the linear model comparison method of Schaeffer (1985). In this method, DYD or de-regressed EBV were used as input data, and international sire EBV were predicted within a mixed linear model structure. The advantage of this method was that relationships between sires in different countries were used, and it was no longer necessary for each sire to have progeny in every country. This greatly

increased the number of bulls included in the analysis, and more modern bulls (i.e., those that were actually being marketed) could be included. Rozzi *et al.* (1990) and Banos *et al.* (1991) applied this method to Holstein data and to Ayrshire and Jersey data, respectively. However, a major limitation of this method was that genetic correlations between all pairs of countries were assumed to be unity, and accounting for genotype by environment interaction was impossible.

This issue was resolved with introduction of the multiple-trait across-country evaluation (MACE) procedure by Schaeffer (1994). With MACE, genetic variances could differ between countries, and genetic correlations between countries could differ from unity. Input data could be DYD or de-regressed EBV, although de-regressed EBV were ultimately used in practice. The MACE procedure is essentially an approximate multiple-trait best linear unbiased prediction (BLUP) model where traits referred to measurements of the same biological parameter (e.g., milk yield) in different countries. It is approximate, because input data are de-regressed national EBV, weighted by the number of progeny, rather than actual daughter performance records. An approximate restricted maximum likelihood (REML) method was developed for estimation of sire (co)variances between countries (Sigurdsson and Banos, 1996), and the International Bull Evaluation Service (INTERBULL) quickly adopted the MACE procedure for routine international dairy sire evaluations.

Routine International Dairy Sire Evaluations. The MACE procedure was applied to Nordic countries in 1994 and extended to other European and North American countries in 1995. Service grew rapidly, from fewer than ten countries initially to twenty-five today. The INTERBULL Centre now evaluates six breeds: Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey, and Simmental. Participating countries include: Australia, Austria, Belgium, Canada, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Israel, Italy, Netherlands, New Zealand, Norway, Poland, Slovenia, South Africa, Spain, Sweden, Switzerland, United Kingdom, and United States of America. Service was initially limited to milk, fat, and protein yield, but in recent years, mastitis resistance (somatic cell count or clinical mastitis) and more than fifteen conformation (type) traits have been added. Genetic correlations between countries for type traits vary dramatically, depending on the (lack of) agreement between the scoring systems applied in different countries.

The MACE procedure offers many advantages, most prominently its ability to accommodate genotype by country interactions and to incorporate genetic relationships between sires in different countries. The latter feature allows all bulls in each member country to be included, regardless of whether or not they have any foreign progeny. Conversion equations can be produced from MACE results, and these are used for cows, heifers, young sires, and embryos, if desired. Perhaps the most important advantage, however, is simplicity. Using MACE, it is possible to express the genetic information of all foreign bulls on the same scale, units, and genetic base as sires with local progeny. Therefore, users can easily compare data of local and foreign bulls without studying the data collection and sire evaluation systems in each country.

Limitations of the Current System. Some of the limitations associated with MACE can be (or have been) corrected via simple modifications to the present system. For example, weighting sire EBV according to the number of progeny is insufficient, because differences exist between sires in the distribution of progeny across herds, the number of lactation records per progeny, the stage of lactation of each progeny, and the number of contemporaries. Fikse and Banos (2001) proposed several weighting factors for national sire EBV within the MACE system. Earlier, Weigel and Banos (1997) considered the amount of historical data to be used and proposed a 'rolling' time edit that eliminates old data as more new data become available. Conventional wisdom would have suggested including all available historical data, but large differences existed between countries in the amount of data used in national evaluations (e.g., some countries had performance data back to 1960, others to 1985). More importantly, these populations were undergoing selection and migration (importation of semen and embryos), and in many cases the dual-purpose Friesian-type sires from the early years were not representative of (nor even related to) the current Holstein populations. Other concerns, such as the impact of heterogeneity of sire variances over time (Canavesi, 2000) and the consideration of multiple lactations as different traits (Sullivan, 2000) have not been resolved.

Other limitations are inherent in the assumptions of the MACE methodology, most notably the assumption that traits (environments) are defined according to country borders. It is obvious that differences exist between herds within large countries (e.g., USA or Australia) in climate conditions and herd management practices, and these can lead to genetic correlations between individual herds or regions that are less than unity (Rekaya *et al.*, 2000). Furthermore, it is unlikely that meaningful genotype by environment interactions exist between small, neighboring countries (e.g., Netherlands and Belgium). Another key assumption is that data editing and genetic evaluation procedures are consistent across countries. Differences in trait definitions (e.g., for type) can be modeled as genotype by environment interactions, but differences in data editing procedures and genetic evaluation models can lead to "false" interactions in which the correlation between sire EBV between countries is less than one, even though the expression of the underlying biological trait is identical.

DIRECT ANALYSIS OF ANIMAL PERFORMANCE RECORDS

International Genetic Evaluation using Multiple-Trait BLUP. One approach to limiting the impact of differences in data editing policies and genetic evaluation models between countries would be direct multiple-trait BLUP analysis of individual animal performance records from participating countries. Weigel *et al.* (2001) analyzed milk yield data from first lactation cows in seventeen countries: Australia, Austria, Belgium, Canada, Czech Republic, Estonia, Finland, Germany, Hungary, Ireland, Israel, Italy, Netherlands, New Zealand, South Africa, Switzerland, and United States of America. Because of concerns about differences in data editing and pre-adjustment of records, these authors used raw test day records from each participating country. Test-day data were combined into lactation yields using the same methodology (Rekaya *et al.*, 1996) for all countries. Extension to a common 305-day lactation length for all countries was impossible, however, because few (if any) cows in many rotational grazing herds reached 305 days in milk. Therefore, records from New Zealand were extended to 270 days, records from Australia, Ireland, and South Africa were extended to 290 days, and

records from all other countries were extended to 305 days. Frequency of milk recording varied widely between herds and between countries, with fewer than four tests per lactation in New Zealand, and more than nine in some European countries. Number of tests per month varied as well, with all milkings weighed in many countries, and a high incidence of alternate AM-PM testing (of milk or components) in others. Similarly, the level of supervision varied from all supervised in some countries to all owner-sampler in others.

Another concern was small contemporary groups. Countries such as Finland and Austria had fewer than five sire-identified, first lactation cows per herd year, and this necessitated new strategies for forming management groups. In that study, fuzzy logic (Rekaya *et al.*, 1999) was used to form herd-year-season groups. If a management group contained fewer than five observations, participation of the corresponding cows was extended to adjacent classes. Each cow had non-zero membership values in up to five adjacent year-season classes within a herd.

The statistical model included effects of herd-year-season, age at calving, milking frequency, heterosis (breed composition of dam) class, sire, and random residual. Genetic correlations between countries were estimated for milk, fat, and protein. Estimated correlations for milk yield ranged from 0.77 between Estonia-Ireland and Estonia-Israel to 0.96 between Australia-Ireland, Australia-New Zealand, and Belgium-Netherlands. Genetic correlations were high (0.91 – 0.96) between rotational grazing countries (e.g., Australia, Ireland, New Zealand) and between high genetic merit countries with intensive management (e.g., Belgium, Canada, Italy, Netherlands, and USA). Correlations between these groups of countries were from 0.80 – 0.90, and correlations between these countries and countries with few genetic ties (e.g., Estonia, Finland, Israel) were often < 0.80. Application of a sire model allowed inclusion of all cows in the analysis, but this simplification is theoretically limiting, due to an inability to account for preferential mating of certain sires to dams of above (or below) average genetic merit.

Due to lactation length differences between herds and between countries, as discussed earlier, a multiple-country test day model was considered by Jamrozik *et al.* (2002a, 2002b). They applied a multiple-trait random regression model to first lactation milk yields of cows from Australia, Canada, Italy, and New Zealand. Genetic (co)variance components of lactation curve coefficients were estimated within and between countries using five-parameter Legendre polynomials. Each sire obtained breeding values for lactation curve parameters, 305-day yield, and persistency on each country's scale. Genetic correlations between countries were slightly lower than the lactation model estimates of Weigel *et al.* (2001). Although computationally challenging, the test-day approach is more appealing theoretically, because extension of records from different management systems to a pre-determined lactation length is not necessary.

Grouping Herds across Country Borders. Although combining performance data into a multiple-trait (by country) BLUP analysis addresses differences in data editing procedures and genetic evaluation models between countries, it does not relax the assumption that traits are defined by country boundaries (Lohuis and Dekkers, 1998). Weigel and Rekaya (2000) proposed a multiple-trait herd cluster model for international genetic evaluation. In this model, management, climate, and genetic variables were used to classify herds from several countries

into groups. Variables included: herd size, calving interval, milking frequency, age at first calving, first lactation milk yield, seasonality of calving, sire PTA milk, percent North American Holstein genes, latitude, altitude, temperature, rainfall, and percentage of arable land used as pasture (the last five variables were assigned by region, rather than herd). These were transformed into principal components (to avoid double counting of correlated variables), and herds were divided into five production systems using cluster analysis. Each group was considered as a different trait in a multiple-trait sire model.

Zwald *et al.* (2001) characterized production systems in the seventeen countries mentioned previously. Differences existed between countries, and between herds within a country, for thirteen management variables: herd size, age at first calving, seasonality of calving, culling rate, peak yield, days to peak yield, persistency, standard deviation of lactation yield, fat:protein ratio, sire PTA milk, percent North American Holstein genes, temperature, and rainfall. Zwald *et al.* (2002) divided herds into quintile groups based on each of these thirteen management variables. Genetic correlations between quintiles were estimated, as an indication of the importance of each management variable with respect to genotype by environment interaction. Covariance functions were fit to the resulting genetic covariance matrices, and the goodness of fit accounted for by a full-fit covariance function relative to a reduced fit (intercept) model was used to quantify the amount of genotype by environment interaction. Zwald and Weigel (2001) then applied the multiple-trait herd cluster model of Weigel and Rekaya (2000) to milk yield data from seventeen countries, and herds were clustered as follows. Each of the thirteen management variables was weighted according to results of the covariance function analysis. Peak yield, herd size, and temperature received the most weight (nearly two-thirds) in the ensuing principal component analysis, and a cluster analysis (based on the values of principle components in each herd) was used to group herds. Genetic correlations between clusters were estimated, and sire EBV were predicted for each environment.

Modeling Environmental Factors on a Continuous Scale. An alternative approach based on reaction norms was proposed by Strandberg *et al.* (2000) and Fikse *et al.* (2002). The reaction norm model is computationally similar to a random regression test day model, but in this case time (days in milk) is replaced by a continuous measure of herd management. A single management variable can be chosen, such as herd average milk yield, or a composite of several variables can be used. Strandberg *et al.* (2000) considered days open and protein yield, while Fikse *et al.* (2002) utilized peak milk yield. In each case, the EBV for a given sire can be computed across a continuum of management levels using regression coefficients obtained from the reaction norm model. This model is more intuitively appealing than the herd cluster model, in that sire EBV can be predicted for a range of environments, and it is not necessary to classify herds into groups. It may be difficult to apply the reaction norm model in more than two or three dimensions, but results of Zwald *et al.* (2002) seem to indicate that peak yield, herd size, and temperature may be sufficient. If more variables were needed, it may be possible to combine them into a “management index”.

Benefits and Limitations of Analysis of Performance Records. The primary advantages of a direct analysis of daughter performance records at the international level are: 1) freedom from country-specific adjustment factors, data editing policies, and genetic evaluation details that might cause bias when data are combined across countries, and 2) freedom to define production environments in an optimal way (either discrete or continuous) regardless of country borders. The primary disadvantages are: 1) computational difficulties that necessitate a more simple (and less accurate) genetic evaluation model at the international level than is utilized by some countries at the national level; 2) difficulty for geneticists at the international level to understand all the complexities of the local climate and herd management conditions (as compared with local geneticists), and 3) a difficulty, at least initially, in understanding the results, because users are accustomed to the 'national' evaluation framework. The second disadvantage is being addressed presently by a joint European project (Canavesi *et al.*, 2001) in which each country will calculate yield deviations for cows in its national system, and these will be subsequently used for international sire evaluation. This system would maintain the national genetic evaluations, and it may lead to better accounting for specific management factors in each country.

CHALLENGES WITH DATA STRUCTURE

Lastly, one should consider the question, "can any methodology provide international dairy sire evaluations of the desired accuracy, given the current limitations in data structure"? For example, Weigel and Powell (2000) examined the international EBV (before importation) and subsequent national EBV (after importation) of more than 600 Holstein sires and showed that MACE was not a significantly better predictor of in-country performance than regression-based conversion equations. One can interpret this as a limitation of the MACE methodology, but it may just be a limitation of the data structure. Weigel *et al.* (2000) showed that many pairs of countries (e.g., Austria-Estonia, Hungary-Israel, etc.) have fewer than ten "common" sires in the Holstein breed. Can we reasonably expect to develop an accurate comparison of bulls from these countries when we have no data available for this purpose? Combining performance data from these countries with that of similar countries in a borderless model or a regional model (Pederson *et al.*, 2001) might help solve the connectedness issue, but such a problem would still exist in a multiple-trait (by country) BLUP model. Other problems, such as data quality (Banos *et al.*, 2001) or preferential treatment of animals that are expected to have high EBV are already a concern within most countries, and it would be naïve to assume that such problems could be easily solved at the international level.

With respect to the desired level of accuracy, the logical question is "accurate enough for whom"? The results from the current MACE system are certainly accurate enough for the commercial dairy farmer who wants to use elite bulls (e.g., the top 5%) to improve the production, type, or udder health of his herd. And the current system can provide a group of potential sires of sons that will lead the major dairy breeds to reasonable rapid genetic progress for the traits of interest. The current system cannot, however, provide enough accuracy for a sire analyst who is making a contract mating, a pedigree breeder who is choosing a sire for embryo transfer work, or a semen marketer who is preparing an advertisement if that person expects to differentiate between bulls with very similar EBV (e.g., within 0.1 genetic SD)

based on progeny groups that differ in location, climate, time, and genetic background of mates. Unfortunately, such expectations seem to exist within the industry, and methods based on daughter performance records are equally unlikely to meet these unrealistic expectations.

Lastly, the question of non-INTERBULL countries arises. The current system serves developed countries very well. If a country already has a national data recording program, a team of well-trained geneticists, and advanced computer hardware and software, it can generate national EBV and participate in the INTERBULL system. In turn, it can receive information about foreign bulls that may be of interest to local farmers and breeding companies. Countries without such an infrastructure (e.g., in Africa or Asia) may also be interested in importing semen, cattle, or embryos, but they cannot make a reasonable comparison of the merit of these candidates with animals from the local breeding population. In many cases, the differences in genetic merit between local and foreign animals are large enough to negate the need for statistical formulae, however, and it is possible for such countries to use the INTERBULL results on the scale of a member country with similar climate and management conditions.

CONCLUSION

International genetic evaluation of dairy sires has come a long way in the past decade, from regression-based conversion equations, to linear model comparisons that can accommodate genotype by environment interactions. Farmers derive many benefits from accurate and understandable genetic data of foreign sires that, although initially tested in another country, can quite easily meet their genetic needs. This system was developed quickly and effectively, through strong cooperation between scientists and industry partners around the world. The next logical step in the evolution of methodology for international genetic comparisons lies in direct analysis of daughter performance records from participating countries. The simplest approach would be a multiple-trait (by country) BLUP analysis of such data, but greater benefits will be derived from borderless models that can estimate sire EBV for each production system, rather than each country. Herds can be grouped into production systems based on known management variables, and then subjected to a multiple-trait BLUP model. Alternatively, management factors can be expressed on a continuous scale and used as independent variables (covariates) in a random regression model, such that sire EBV can be predicted for the specific conditions present in any herd. Limiting factors include a lack of knowledge among scientists at the international level about specific management factors present within each country, and the need to use a computationally feasible, but perhaps technically less satisfying, model at the international level due to the tremendous size of the global data set. In addition to technical challenges, there are political challenges involved in a partial transfer of responsibilities from the national level to an international center. In the meantime, we will likely see a continued evolution of the dairy genetics industry from small regional cooperatives to large multinational companies, and this raises the possibility of proprietary data collection and animal evaluation systems that may not be part of public national and international genetic evaluation systems.

REFERENCES

- Banos, G., Schaeffer, L.R., and Burnside, E.B. (1991) *J. Dairy Sci.* **74** : 1060-1068.
- Banos, G., Wiggans, G.R., and Powell, R.L. (2001) *J. Dairy Sci.* **84** : 2523-2529.
- Canavesi, F. (2000) *INTERBULL Bull.* **25** : 31-40.
- Canavesi, F., Boichard, D., Ducrocq, V., Gengler, N., De Jong, G., and Liu, Z. (2001) *INTERBULL Bull.* **27** : 32-34.
- Goddard, M.E. (1985) *Livest. Prod. Sci.* **13** : 321-331.
- Fikse, W.F., and Banos, G. (2001) *J. Dairy Sci.* **84** : 1759 – 1767.
- Fikse, W.F., Rekaya, R., and Weigel, K.A. (2002) *Livest. Prod. Sci.* (submitted).
- Jamrozik, J., Schaeffer, L.R., and Weigel, K.A. (2002a) *J. Dairy Sci.* (submitted).
- Jamrozik, J., Schaeffer, L.R., and Weigel, K.A. (2002b) *J. Dairy Sci.* (submitted).
- Lohuis, M.M., and Dekkers, J.C.M. (1998) *Proc. 6th WCGALP XXVI* : 169-172.
- Mattalia, S., and Bonaiti, B. (1993) *INTERBULL Bull.* **8** : 66-69.
- Pederson, J., Langdahl, C., Poso, J., and Johansson, K. (2001) *INTERBULL Bull.* **27** : 3-8.
- Rekaya, R., Alenda, R., Bejar, F., and Carabano, M.J. (1996) *Frisona Espanola* **94** : 33-42.
- Rekaya, R., Weigel, K.A., and Gianola, D. (1999). *J. Anim. Sci.* **77 (Suppl. 1)** : 33.
- Rekaya, R., Weigel, K.A., and Gianola, D. (2001) *J. Dairy Sci.* **84** : 1525-1530.
- Rekaya, R., Weigel, K.A., and Gianola, D. (2000) *J. Dairy Sci.* (submitted).
- Rozzi, P., Schaeffer, L.R., Burnside, E.B., and Schlote, W. (1990) *Livest. Prod. Sci.* **24** : 15-20.
- Schaeffer, L.R. (1985) *Livest. Prod. Sci.* **12** : 105-112.
- Schaeffer, L.R., (1994) *J. Dairy Sci.* **77** : 2671-2678.
- Sigurdsson, A., and Banos, G. (1996) *J. Dairy Sci.* **79** : 1117-1125.
- Strandberg, E., Kolmodin, R., Madsen, P., Jensen, J., and Jorjani, H. (2000) *INTERBULL Bull.* **25** : 41-45.
- Sullivan, P.G. (2000) *INTERBULL Bull.* **25** : 13-17.
- Weigel, K.A. (1997) *J. Dairy Sci.* **80** : 3420-3424.
- Weigel, K.A., and Banos, G. (1997) *J. Dairy Sci.* **80** : 3425-3430.
- Weigel, K.A., and Powell, R.L. (2000) *J. Dairy Sci.* **83** : 1081-1088.
- Weigel, K.A., and Rekaya, R. (2000) *J. Dairy Sci.* **83** : 815-821.
- Weigel, K.A., Rekaya, R., Zwald, N.R., and Fikse, W.F. (2001) *J. Dairy Sci.* **84** : 2789-2795.
- Weigel, K.A., Rekaya, R., Zwald, N.R., and Gianola, D. (2000) *INTERBULL Bull.* **25** : 26-30.
- Wilmink, J.B.M., Meijering, A., and Engel, B. (1986) *Livest. Prod. Sci.* **14** : 223-229.
- Zwald, N.R., and Weigel, K.A. (2002) *J. Dairy Sci.* (submitted).
- Zwald, N.R., Weigel, K.A., Rekaya, R. (2002) *J. Dairy Sci.* (submitted).
- Zwald, N.R., Weigel, K.A., Fikse, W.F., and Rekaya, R. (2001) *J. Dairy Sci.* **84** : 2530-2534