THE USE OF INTERNATIONAL GENETIC MATERIAL IN AN IMPORTING COUNTRY

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INTRODUCTION

The ability to move semen, embryos or live animals between countries provides the opportunity to select breeding stock from an international gene pool. This opportunity is already being utilised in Holstein cattle and will increasingly be utilised by other breeds and species in the future. The advantage of access to a wider range of genotypes must be compared with the disadvantages of higher cost, reduced suitability to local requirements and reduced effective population size of the breed internationally. The aim of this paper is to consider the criteria that should be used in selecting animals for importation and the way in which these animals should be used in the importing country.

The criteria that we consider are:

- Estimated Breeding Value (EBV) for the local breeding objective
- cost
- heterosis, inbreeding depression and genetic variance
- reliability of EBV

The use of EBVs to select stock for importation implies that EBVs for animals in other countries can be compared with EBVs for local animals. Therefore the first topic reviewed is that of international genetic comparisons.

INTERNATIONAL GENETIC COMPARISONS

Joint Analysis of Data

If datasets from different countries are not too large and there are genetic links between them, the simplest approach is simply to calculate EBVs from the combined data. However disadvantages of this may include the need for different statistical models for data from different countries, different genetic parameters, sire x country interactions, less efficient error detection and lack of local control of the manner in which the results are released. Despite these disadvantages this is still an attractive method in some cases.

Conversion Formulae

EBVs calculated in different countries cannot be directly compared because they are expressed relative to different bases and predict performance under different conditions. EBVs can be converted between countries with simple linear formulae such as

$$EBV_j = a + b\ EBV_i$$

where
EBV_i = EBV in country of origin (i)
EBV_j = estimated breeding value in country j.

Methods for calculating a and b have been proposed by Goddard (1985) and Wilmink et. al (1986) and both are approved by 'Interbull' for use in dairy cattle. These methods account for differences between countries in the

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base used and in the genetic and phenotypic variances, and they allow for the genetic correlation between performance in the two countries to be less than 1.0. They rely on data from bulls which have been progeny tested in both countries. However, they differ from the simple regression of EBV in importing country on EBV in original country because they make proper allowance for the reliability of the EBV in the importing country. Some of the problems encountered with use of conversion formulae are reviewed by Jones and Goddard (1990).

If a foreign sire has some local offspring there are then two estimates of his local breeding value : the conversion from his home country EBV and the EBV based on local data. If he has only a small number of local offspring his local EBV can substantially underestimate his true breeding value. To overcome this problem Goddard and S. Smith (unpublished) developed a Baysian method for incorporating the converted EBV as prior information into the local system of EBV calculations. The reliability ascribed to this prior is approximately r_g^2 times the reliability of the EBV in the home country where r_g is the genetic correlation between performance in the two countries. Consequently once a sire has a large number of local offspring these dominate the EBV and the converted EBV has little effect. The major problem associated with use of the converted EBV as a prior is to avoid 'double counting' of relationship information in both the home country and importing country EBV calculations. Goddard and Smith devised methods to overcome this problem and these are discussed by Jones and Goddard (1990).

Incorporating converted EBVs into the local evaluation also improves the accuracy of the EBV of local animals whose parents have only foreign EBVs. This occurs frequently in dairy cattle where many young bulls and potential bull dams have North American sires.

International Genetic Evaluations

Conversion equations deal with only 2 countries at a time. However, some sires may have offspring in many countries. To combine all the information into one EBV, Schaeffer (1985) and Banos et al (1990) proposed use of an international analysis which used the results from each within-country genetic evaluation as input data. They assumed $r_g = 1$ but Schaeffer and Zhang (1993) have recently extended the model to a multi-trait analysis in which performance in each country is a different trait with r_g not necessarily 1.0. Banos (these proceedings) discusses such international genetic evaluations.

Estimates of r_g for milk yield between Australia and other countries are approximately 0.8. Visual evidence that r_g is less than 1.0 can be seen by plotting the EBVs of bulls with reliability of EBV above 90% in both Canada and Australia. Some bulls deviate significantly from the regression line. This could be due to a true genotype by environment interaction ($r_g < 1.0$) or to bias in either the Australian or Canadian EBVs of some bulls or to different models used in the 2 countries. The presence of significant reranking of bulls between Canada and New Zealand in experimental data (Petersen 1988) suggests that r_g is truly less than 1.0 in that case.

If r_g is assumed to be 1.0 then the international EBV of a sire is dominated by the performance of offspring in the country where he has the most offspring. However if a multi-trait model with $r_g < 1.0$ is used and a sire has a large number of offspring in country i, then his international EBV for performance in country i will be dominated by the performance of his offspring in that country. This appears to us to be a desirable property.

In the models suggested for international genetic evaluations, sires have been grouped by year of birth and country of origin. This may present some problems in the multi-trait model because a group solution is required for every trait. For instance, a solution is needed for sires born in country i in 1980 for performance in country j. In many cases few sires in this group will have offspring in country j and so the group solutions will be estimated with large standard errors.

Since the group solutions form part of the EBV of each sire this is a serious problem. For instance, consider the EBVs, for performance in country j, of 2 sires from country i born in different years. Although neither has offspring in country j the order of their EBVs might be the reverse of the order in their home country due to anomalous group solutions for performance in country j.

Schaeffer and Zhang (1993) suggests treating the groups as random effects. Although they do not specify the variance structure, it would presumably be similar to that used for individual sire effects. This would have the effect of making group solutions for performance in countries i and j more similar than if the group effects were treated as fixed. However, it might have other consequences such as underestimating genetic trend because group solutions are all regressed toward a common mean.

Goddard (1992a) suggested an alternative approach to this problem in which group solutions are constrained. For instance, let

$\hat{g}_{jik}$ = group solution for performance in country j of bulls born in country i in year k

b = genetic regression of performance in country j on performance in country i.

Then constrain the solutions such that

$\hat{g}_{jik} - b\hat{g}_{iik}$ = constant for all k

This constraint causes the group solutions to convert between countries in the same way as individual sire solutions. This ensures that the EBVs of bulls which have no relatives outside country i will remain in the same order in all other countries. This property occurs automatically when conversion equations are used because the equation is applied directly to the EBV (= group + individual solutions) so that group solutions are converted in the same way as individual solutions. Goddard (1992a) discusses briefly the implications of applying these constraints to groups from different countries instead of different years within a country.

Conversion equations and international genetic evaluations require genetic links to exist between animals in different countries. In the dairy industry the most direct links come from sires which have daughters in two or more countries. However, the daughters born from imported semen may receive preferential treatment causing a bias in the EBV of the sire. For this reason Interbull use only the daughters of a bull in his home country in their international genetic evaluation. Therefore they rely on links created by sires having progeny tested sons (i.e. grand daughters) in more than one country.

We have compared the effect of using all offspring or excluding Australian daughters of foreign sires in calculating a conversion equation from Canada to Australia. Two sets of EBVs for performance in Australia were calculated. One used all records and one excluded daughters of bulls standing in other countries. In order to minimise statistical noise in the EBVs we have used only EBVs with greater than 90% reliability in both Canada and Australia. There were 91 bulls that met this criterion when all offspring were included (dataset 1) and 11 when Australian daughters of foreign bulls were excluded (dataset 2). All these were Canadian bulls. The results of the regression analysis are presented in table 1. For dataset 2 the regression was calculated using EBVs calculated with and without inclusion of daughters of foreign bulls.

Both the intercept and regression coefficient declined when daughters of foreign bulls were excluded from the EBVs providing evidence that this removed some bias. This occurred because the EBVs of 10 of the 11 bulls declined when their Australian daughters were excluded. However the regression coefficients from both analyses of dataset 2 were higher than that from dataset 1 and had larger standard errors. Although it may contain

some bias, the regression estimated from dataset 1 appears to be the most accurate because so much more data is available. Although 11 bulls is a small dataset there will be many countries with less than 11 sires, from each other country, who have enough local progeny tested sons to give the sire a reliable EBV.

Table 1.   Regression of milk fat EBV in Australia on Canadian Sire Proof

| Australian Daughters | Dataset 1 (N=91) | | | Dataset 2 (N=11) | | |
of foreign bulls	a	b	r	a	b	r
included	18.8	1.45	.84	24.4	1.83	.90
	(7.8)	(0.10)		(8.2)	(0.29)	
not included				18.9	1.54	.90
				(7.3)	(0.26)	

Regression equation y = a + bx; r = correlation coefficient; standard errors in brackets

Dataset 1 = bulls with reliability >90% in both countries
Dataset 2 = bulls with reliability >90% in both countries when daughters of foreign bulls are excluded

In an international genetic evaluation the covariance structure from which b could be calculated is assumed known (i.e. it must be estimated prior to the BLUP) while the means of genetic groups, corresponding to a, are estimated within the BLUP calculations. Excluding daughters of foreign bulls will reduce the precision with which group effects are estimated although it may eliminate some bias. Genetic correlations are always difficult to estimate and excluding this data when estimating the covariance matrices may well lead to very poor estimates.

Thus, in the design of international genetic evaluations, questions concerning the genetic grouping strategy and the data that should be included for the estimation of covariance structures and the prediction of breeding values remain unresolved.

Integration of International and Within Country Evaluations
It is possible that the international EBVs discussed above could replace within country EBVs. However, it seems to us better to retain local calculation and release of within country EBVs. Then each country can control the timing of release and the traits analysed, and detection of errors is likely to be more successful when it is carried out closer to the source of the data. If within country EBVs are retained they should be integrated with the international EBVs. For instance, if within country EBVs are based only on local data while international EBVs use all data, then the international EBVs should be more accurate than the local EBVs. If that were so wise breeders would use the international EBVs and ignore the local EBVs.

Goddard (1992a) suggested a method of integrating national and international genetic evaluations which is illustrated in figure 1. Each country sends results from its own genetic evaluation to the international centre as well as releasing EBVs. The international centre calculates international EBVs using a multi-trait model and returns the results to each participating country. The participating countries use these results as prior information in the next round of national genetic evaluations.

A potential problem with this suggestion is that information will be 'reused' each time it goes around the loop. For instance, if foreign information is incorporated into local EBVs in country i and these local EBVs are then transmitted to the international centre, the foreign information could be treated as if it were independent data from country i. One way to overcome this problem is to transmit local daughter yield deviations (DYD) from the

local to the international centre. The multi-trait analysis of Schaeffer and Zhang (1993) is designed to use DYD as input data. A method must also be found to avoid a country using international EBVs as prior information which include their own DYD. This could be achieved by the international centre calculating a series of EBVs in which the data from each country is omitted in turn. Alternatively a country could use the international EBVs and their own data to deduce the additional information that has been added.
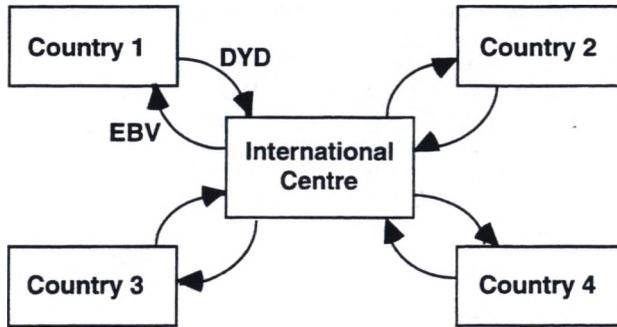

Figure 1.   A proposed method of integrating national and international genetic evaluations

CRITERIA FOR SELECTION OF FOREIGN ANIMALS

EBV for Local Breeding Objective

The simplest approach is to select animals, regardless of country, on EBV for the local breeding objective (EBV_T). This requires that EBVs for individual traits be combined to give an EBV_T. This takes account of 2 different aspects of adaptation to local requirements. Firstly the individual EBVs should come from a multi-trait analysis so that they are EBVs for local performance. Secondly, the objective should include traits and economic weightings which are appropriate to local conditions.

This criterion balances the advantages of high production against the disadvantages of lack of local adaptation. Unless foreign and local populations happen to have a similar mean EBV_T, it will result in either a very high or very low level of importation. However other considerations modify this conclusion.

If the breeding objective is non-linear in some traits this might modify the way in which imported animals are used. Moav and Hill (1966) and Goddard (1983) point out that the optimum direction of genetic change under a non-linear objective depends on the time horizon adopted. For a trait whose economic value exhibits a pattern of decreasing returns (ie the economic weight decreases as the mean increases), the optimum selection emphasis decreases as the time horizon lengthens. For example consider a situation in which a certain level of resistance to a disease is valuable but further improvements beyond this level are unnecessary, and the present population mean is just below the required level. If the goal is short term improvement emphasis must be given to disease resistance. But from a long term perspective, resistance can be improved more slowly and more emphasis given to other traits.

The appropriate time horizon depends in part on how the selected animal will be used. In dairy cattle a shorter time horizon is justified when selecting bulls to breed commercial cows than when selecting bulls to breed bulls. More generally the higher in the stud pyramid an animal is to be used the longer the time horizon that can be justified because the greater the number of generations of selection that will occur before production of commercial descendants.

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Cost

To justify investment in breeding stock the benefits should outweigh the cost. The benefits depend on the economic value of an animal's genotype (EBV_T) times the number of discounted expressions of that genotype if selected (McClintock and Cunningham 1974). Wade and Goddard (1994) showed how this concept could be applied to decisions on the purchase of animals, semen or embryos. They also showed that as animals are used higher in the stud pyramid the number of discounted expressions increases. Thus, in dairy cattle, a high semen price may be justified for bulls to breed bulls but not for bulls to breed cows.

Heterosis, Inbreeding and Genetic Variance

If the imported animal is of a different breed to the local population his offspring may benefit from heterosis. Even within a breed, an imported animal will be at an advantage if he is less closely related to the local population than local competitors. In the future this will be one factor preventing local populations of Black and White dairy cows from becoming closed to imports (Goddard 1992b).

Heterosis and inbreeding depression are most relevant in commercial animals. Changes in genetic variance are more relevant in stud animals. The disadvantage of reduced genetic variance due to inbreeding is well recognised but there is less scientific emphasis given to increased genetic variance in segregating crossbreds and little experimental data for breeds of livestock.

Goddard and Smith (1990) described how selection could be based on the EBV of a sire adjusted for the inbreeding depression of the offspring. That is, selection is based on the criterion

$$\frac{1}{2}EBV - bF$$

where EBV = EBV of sire, F = inbreeding coefficient of prospective offspring and b is the inbreeding depression per unit of inbreeding coefficient. Wray and Goddard (unpublished) have extended this approach to account for the effect of reduced genetic variance on long term genetic gain. However there has been little study of how inbreeding should be treated by one breeding program (eg country) which exchanges genetic material with other programs. On the one hand long term inbreeding could be ignored on the grounds that new genetic lines can always be obtained from elsewhere. However if the same sires are being used in all countries (as has occurred with Holstein cattle) this may not be true. Alternatively if this country is using different sires to the rest of the world it is presumably because they are superior for local requirements and therefore introduction of genetic material from elsewhere to avoid inbreeding will lead to a reduction in EBV_T. Consequently the safest policy may be to treat the local breeding program as if it were closed when predicting future inbreeding.

Reliability of EBV_T

The reliability of EBV_T can be low either because the EBV of individual traits is of low reliability or because there is no EBV for some traits of value locally. The risk of a selection response much worse than expected can be reduced by selection of animals with highly reliable EBV_T. However in some situations selection of animals with lowly reliable EBV_T may be advantageous. For instance, when selecting bulls to progeny test a low reliability implies a greater chance of having a very high (or very low) EBV after progeny test.

CONCLUSION

Imported genetic material can offer a country a wide range of options. The most important criterion when selecting animals to import is EBV for the local breeding objective. To use this criterion a system of comparing the breeding value of animals from different countries is needed. This can be accomplished by joint analysis of the data from different countries, equations which convert EBVs between countries or an international analysis of the results of within country genetic evaluations. Goddard (1992a) compares the advantages of these 3

alternatives. If international trade in genetic material is widespread a system which integrates international and local genetic evaluations is desirable. This system should allow the genetic correlation between performance in different countries to be less than 1.0 by using a multi-trait model. No international genetic comparisons are possible unless data with adequate genetic linkages across countries is available. For this reason alone international genetic evaluations are most advanced for dairy cattle but other industries may follow the same path eg beef cattle.

Other criteria such as cost, inbreeding, outcrossing and the reliability of EBVs should influence the selection of material to import and also the way in which it is used within the country.

It is not uncommon for imported animals or semen or embryos to be used at a high level in the stud pyramid while local animals are used at a lower level such as for breeding commercial offspring. The selection criteria discussed could provide a rational justification for this. For instance, it might be justified to purchase expensive semen to breed young bulls from a sire with high EBV for milk yield but no EBV for traits of local adaptation in the belief that some of his sons will have the minimum level of adaptation necessary. However we believe a quantitative analysis of the factors discussed should be carried out before departing from the simple policy of selecting the animals with the highest EBV_T adjusted for cost.

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