Partitioning of International Genetic Trends by Origin in Brown Swiss Bulls

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Abstract

Breeders improve their population by domestic selection and/or import of animals from foreign populations. Assessing the impact of these two sources is important to understand the sources of genetic changes (good or bad) in population. Partitioning breeding values by the origin of Mendelian sampling terms is a possible way to address this issue. We describe this method and apply it to international Multiple Across Country Evaluation in Brown Swiss breed. Partitioning of global genetic trends for the population of bulls and their ancestor revealed a large impact of USA on increased production as well as on decreased somatic cell score and fertility. The trend for somatic cell score has been reversed by the same country. Other countries have achieved smaller genetic gains in production and maintained no change in somatic cell score and fertility.

Keywords: genetic trend, partitioning, production, fertility

Introduction

Breeds of cattle went through large changes over the course of history. Breeders improved traits of interest with domestic selection and/or import of foreign animals from (potentially) better populations. With the advent of insemination the later method of improvement is easy to perform. In such setting the international comparison of sires (Schaeffer, 1994) is of vital importance for objective comparisons. The amount of germplasm exchange varies widely as some countries tend to rely on import more than other countries. In addition to this each country might also perform national selection with varying gains due to several factors (size of population, selection intensity, breeding objective, …).

Inferring the effect of each country (origin) on national and international genetic trend is in theory possible with a long-term experiment, but highly impractical due to the formidable costs and logistics of such an experiment. Therefore, alternative ways are needed to gain insight into country contributions. The method of partitioning breeding values by paths of selection as proposed by Garcia-Cortes *et al.* (2008) is easy to adopt for such analyses.

The objective of this work was to apply the method of Garcia-Cortes *et al.* (2008) to assess the contribution of different countries to global genetic trend in Brown Swiss bulls. First the method is described and demonstrated with a small example. Furthermore application results are presented with discussion.

Method

Any kind of pedigree based mixed model (animal model, sire-maternal grandsire model, …) is based upon the prior model for breeding values using the recursive system of equation. For animal model the core equation is:

$$a_i = 1/2\, a_{s(i)} + 1/2\, a_{d(i)} + w_i , \qquad (1)$$

where a_i, $a_{s(i)}$, $a_{d(i)}$ are breeding values of individual animal and their parents, respectively, while w_i is individuals' deviation from parent average, i.e., the Mendelian sampling term. For base population members $a_i = w_i$. In matrix notation (1) can be written as:

$$\mathbf{a} = \mathbf{Tw}, \tag{2}$$

where $\mathbf{T}$ describes flow of genes through pedigree (e.g., Henderson, 1976; Woolliams *et al.*, 1999). Equation (2) shows that breeding values are a linear combination of Mendelian sampling terms and that the same equation can be used also for predictors of $\mathbf{w}$, i.e., $\hat{\mathbf{a}} = \mathbf{T}\hat{\mathbf{w}}$.

Garcia-Cortes *et al.* (2008) proposed to define a set of k partitions, such that:

$$\mathbf{P}_1 + \mathbf{P}_2 + \ldots + \mathbf{P}_k = \mathbf{I}. \tag{3}$$

Using (3) and the fact that $\mathbf{w} = \mathbf{T}^{-1}\mathbf{a}$ they wrote (2) as:

$$\begin{aligned}\hat{\mathbf{a}} &= \mathbf{TP}_1\mathbf{T}^{-1}\hat{\mathbf{a}} + \ldots + \mathbf{TP}_k\mathbf{T}^{-1}\hat{\mathbf{a}}, \\ &= \hat{\mathbf{a}}_1 + \hat{\mathbf{a}}_2 + \ldots + \hat{\mathbf{a}}_k,\end{aligned} \tag{4}$$

where $\hat{\mathbf{a}}_i$ are partitions of $\hat{\mathbf{a}}$ according to the definition of (3). These partitions can be summarized separately to obtain the partitioning of total genetic trend.

Once we have $\hat{\mathbf{a}}$ from the routine genetic evaluation, the computation of (4) is very simple and involves only 1) computation of inferred Mendelian sampling terms $(\hat{\mathbf{w}})$ and 2) dropping $\hat{\mathbf{w}}$ through pedigree according to (3). We implemented this in the R package partAGV, which eases the computation and presentation of results.

The same approach can also be used for other pedigree based mixed models such as sire-maternal grandsire model with slightly modified computational steps. When genetic evaluation model includes genetic groups (Quass, 1988) their effect is automatically propagated through the pedigree and all the above derivations still hold (e.g., Woolliams *et al.*, 1999).

Another use of this method is for the analysis of gene proportions by origin. For such an analysis we simply need to set $\hat{\mathbf{a}} = \mathbf{1}$ and evaluate (4). The trick is that by doing this we implicitly set all Mendelian sampling terms to zero expect for the base population and therefore applications of (4) traces the flow of genes through the pedigree.

Example

A small example (Table 1) will serve as demonstration. According to (2) we can write:

$$a_C = 1/2\, w_A + 1/2\, w_B + w_C,$$

where animals A and C were born and registered (and therefore selected) in country X, while animal B was born and registered (and therefore selected) in country Y. If we define partitions according to countries and use (4) we can write:

$$\begin{aligned}a_C &= (1/2\, w_A + w_C) + 1/2\, w_B, \\ &= (50 + 1) + 53 = 51 + 53, \\ &= a_{C,X} + a_{C,Y},\end{aligned}$$

where $a_{C,X}$ $(a_{C,Y})$ is the partition of animals' C breeding value that could be attributed to country X (Y).

Table 1. Small example.

Animal	Sire	Dam	Country	BV
A	/	/	X	100
B	/	/	Y	106
C	A	B	X	104
D	/	/	Y	106
E	C	D	X	103

BV – breeding value

For animal E we can write:

$$\begin{aligned}a_E &= 1/2\,(1/2\, w_A + 1/2\, w_B + w_C) + 1/2\, w_D + w_E, \\ &= (1/4\, w_A + 1/2\, w_C + w_E) + (1/4\, w_B + 1/2\, w_D), \\ &= (25 + 0.5 - 2) + (26.5 + 53) = 23.5 + 79.5, \\ &= a_{C,X} + a_{C,Y}.\end{aligned}$$

The percentage of genes in animal E is 25% (75%) from country A (B), while the additive effect (value) of these partitions is 23.5 (79.5) or 23% (77%).

Assumptions

The use of presented method for the analysis of country contributions to each breeding value rests on the following assumptions:

A) All partitions represent contribution of each country relative to defined base population in genetic evaluation. Setting base population at some point in time removes any previous contributions.

B) Input values $\hat{\mathbf{a}}$ are properly describing the underlying state of nature, e.g., there are no biases in $\hat{\mathbf{a}}$ due to the potential non-additive and preferential treatment effects.

C) Mendelian sampling term of animal selected in country X can be attributed to this country. This can be defended from the fact that selection decision is done by country X and they should be praised/blamed for introduction of this animal in population. When this decision is done on objective information, e.g., progeny test, it is clear that country X invested in the (incomplete) discovery of animals' Mendelian sampling term and should therefore be accredited for this. Objective selection on one trait can lead to decrease of non-measured negatively correlated traits, which implies that country X should be "accredited" also for such contribution albeit negative and non-intentional. Therefore, the same can be assumed also for decisions based on "non-objective" information.

D) With time evaluations of Mendelian sampling terms converge (e.g. Bijma and Wooliams, 2000) and due to assumption C) we can still accredit these terms to countries carrying out selection decisions.

Material

Presented method was applied to Multiple Across Country Evaluation (MACE; Schaeffer, 1994) breeding values for Brown Swiss breed on Swiss scale. The April 2011 experimental run of the so called sire-dam core MACE was used, which is essentially a MACE animal model for bulls, i.e., the deregressed national breeding values of bulls are being modelled, while the pedigree includes both sire and dam pedigree sides of these bulls.

Analysis focused on the following traits:

- production trait - protein yield (PRO; a trait with steep positive global genetic trend),
- health trait - somatic cell score (SCS; a trait with negative global genetic trend with improvement),
- fertility trait - lactating cows' ability to conceive (CC1; a trait with negative global genetic trend), and
- longevity trait - direct longevity (DLO; a trait with variable genetic trend).

Pedigree and breeding values were obtained along with country of registration information for each trait. Around 30,000 animals were in pedigree (Table 2) with birth years from 1960 to 2006. Animals born in year 2006 were merged with animals born in 2005 due to the low number. Origins with the largest number of animals were Switzerland (CHE), Germany (DEU), Austria (AUT), Italy (ITA), and United States of America (USA). These origins had sufficient animals in all trait analyses. France (FRA) and Slovenia (SVN) had smaller number of animals and only for some traits due to the lack of their participation in MACE. Other countries with even smaller number of animals were merged in one origin (OTH; Table 2).

Table 2. Number of animals (sires and dams) in pedigree by origin and trait.

	Trait			
Origin	PRO	SCS	CC1	DLO
AUT	7405	6397	6564	7585
CHE	8900	8720	8846	9051
DEU	8403	8372	8219	8631
FRA	542	533	/	509
ITA	4413	4097	827	4375
SVN	600	/	/	/
USA	2904	2837	2154	2892
OTH	163	159	176	160
All	33330	31115	26786	33202

OTH – other countries (AUS, BEL, CAN, GBR, NLD, NZL and for some traits FRA and SVN)

Prior to analysis breeding values were centered so that the mean in year 1960 was zero and scaled with CHE scale and trait specific additive genetic variance in order to ease interpretation. For each trait we computed breeding value partitions according to (4) with partitions being defined by the country (origin) of animals' registration (AUT, CHE, DEU, FRA, ITA, SVN, USA, and OTH). To gain insight into country partitions over different periods another partitioning was by country and period, where periods were 1960-1980, 1981-1990, 1991-2000, 2001-2005. The first period was chosen due to the fact that pedigree data in Brown Swiss MACE is available from 1960 onwards, while "phenotype" information is used only from 1981 onwards. Other periods were chosen such that they covered 10 years, if possible.

Results and Discussion

Proportion of genes by origin

Initially the analysis of the proportion of genes by origin was performed based on the most complete pedigree from protein yield evaluation. These values as well as any other values presented in results represent state in the global bull population and their relatives. From year 1960 onwards the proportion of genes originating from USA is steadily increasing from about 15% to 84% (Figure 1). On the other side the proportion of genes originating from CHE has decreased as well as for other origins. In last five years the average proportions of genes were: USA 84%, DEU 9%, CHE 4%, AUT 1% and less for other origins.

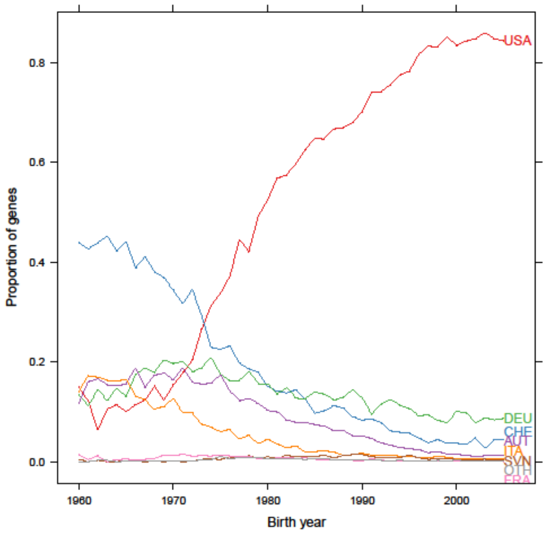

Figure 1. Proportion of genes by origin from 1960 onwards.

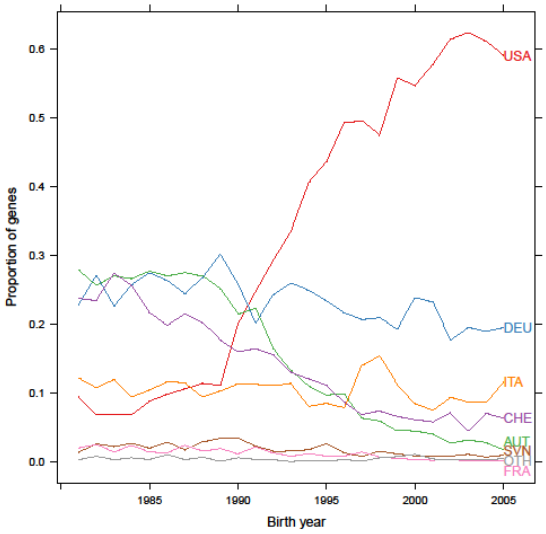

Figure 2. Proportion of genes by origin from 1981 onwards.

These results nicely show the development of modern Brown Swiss breed. Brown cattle originate from the Alpine region in Europe where it was kept as a dual purpose breed. In the late 19th century only a minor number of animals were imported to USA and intensively selected towards dairy type and then after 1950 continually exported back to Europe for upgrading local populations (e.g., Felius, 2007). As pedigree information is available only from 1960 onwards we only observe the increase of proportion of USA genes, which are in fact originating from Europe. The proportions of genes by origin from base population set to year 1981 show substantial changes (Figure 2). These results clearly show the importance of understanding that results are relative to defined base population (assumption A).

Genetic trends by origin

Selection on protein production has been very successful. The change has been 3 genetic standard deviations (GSD) and it seems that selection limits are not yet reached (Figure 3, Table 3). Partitioning of global genetic trend reveals that the majority of progress has been achieved by selection in USA (1.79 GSD), followed by DEU (0.62 GSD), ITA (0.20 GSD), CHE (0.17 GSD), and AUT (0.06 GSD).

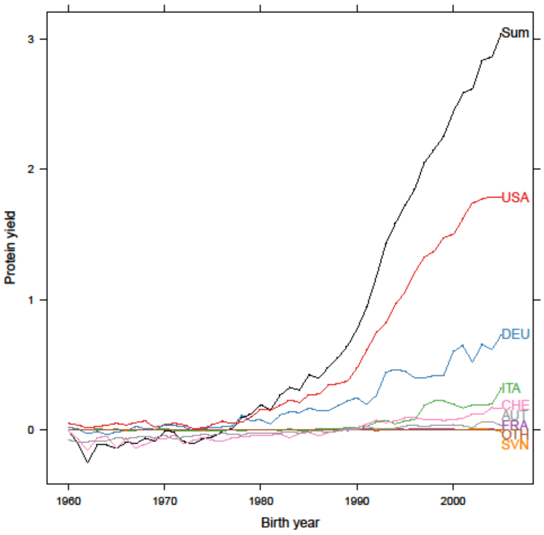

Figure 3. Partitioning of global genetic trend by origin for PRO.

Genetic trend for somatic cell score (Figure 4, Table 3) is in contrast to protein yield negative up to 1995 (-0.8 GSD). From that point the trend has been reversed (-0.4 GSD). Partitioning revealed that the contribution of USA is by far the largest for decrease as well as for the reversion phase.

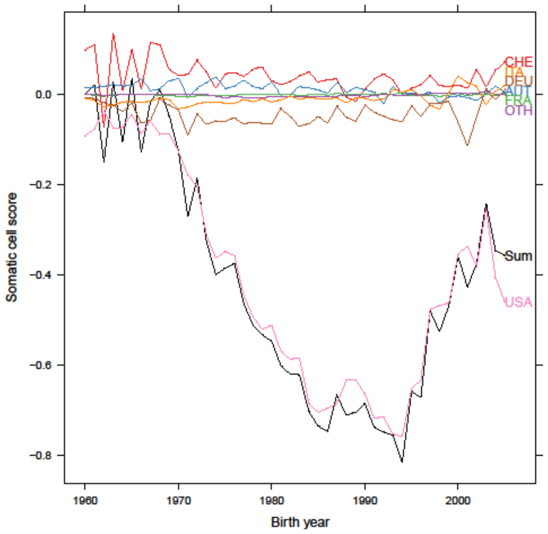

Figure 4. Partitioning of global genetic trend by origin for SCS.

Decrease in fertility traits is a common side phenomenon of selection on milk production in dairy cattle. Brown Swiss breed is no exception (Figure 5, Table 3). The change has been almost -0.6 GSD and again the main partition was accredited to USA, while other countries did not contribute largely to changes in this trait.

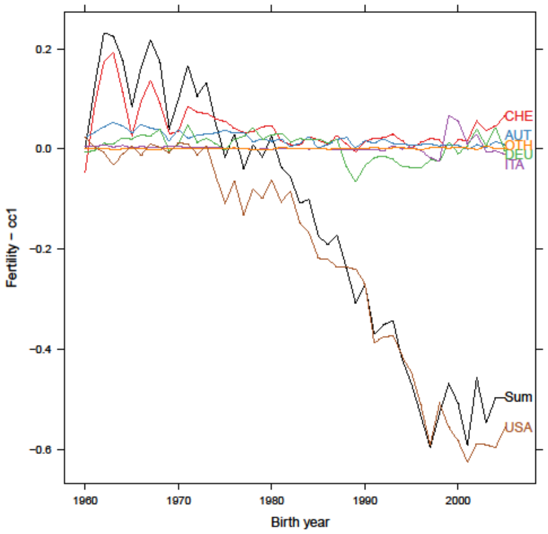

Figure 5. Partitioning of global genetic trend by origin for CC1.

Genetic changes in direct longevity were of much smaller magnitude (Figure 6, Table 3). It seems that contribution from USA is again the major driving force in global genetic change after 1995.

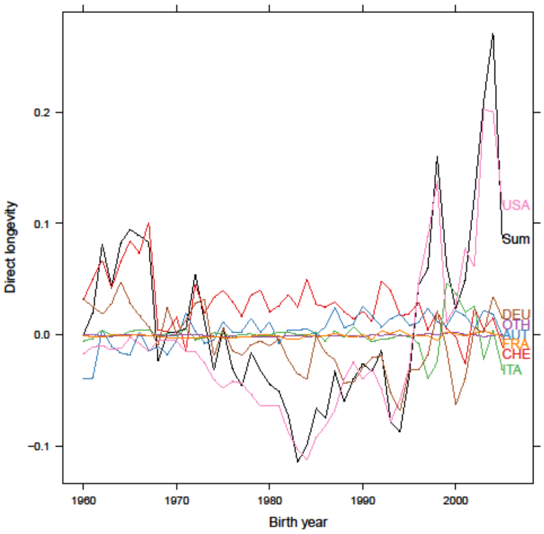

Figure 6. Partitioning of global genetic trend by origin for DLO.

Recent results of Pimentel *et al.* (2010) in Holstein breed and Olsen *et al.* (2011) in Norwegian Red breed show that there are genome regions harbouring QTLs with pleiotropic effects on milk production and fertility and that some of them are antagonistic but not all. This provides opportunities for selection, which would not be accompanied with negative effects in correlated traits.

Conclusion

Partitioning of breeding values according to origin provides a way to assess country contributions to genetic gain. This enables analysis of domestic versus national selection impact for national analyses and country impact comparisons for international analyses. Results from this work show that breeding performed by USA had substantial impact on Brown Swiss breed – improved protein production, but also decreased somatic cell score and fertility. However, trend for the later trait has been reversed by the same country. Other countries achieved lower genetic gains in protein production and maintained no changes in somatic cell score and fertility.

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