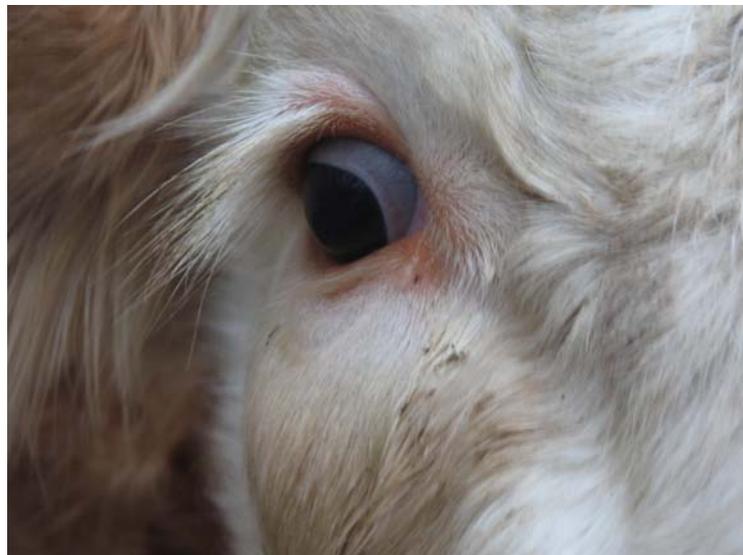Swedish University of Agricultural Sciences

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International and national genetic evaluation of beef cattle - validation of national genetic evaluation models

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Internationell och nationell avelsvärdering av köttdjur
- validering av nationella avelsvärderingsmodeller

Jenny Ahlqvist

Table of contents

List of abbreviations

AGBU	Australian University of New England
AI	Artificial Insemination
AIC	Akaike's Information Criterion
AICC	the Corrected Akaike Information Criterion
BASCO	Beef and Sheep Company
BIC	Schwarz' Bayesian Information Criterion
BLUP	Best Linear Unbiased Prediction
BV	Breeding Value
CMMS	Calf registration and animal Movement Monitoring
CRL	Community Reference Laboratory
DEFRA	Department for Environment, Food and Rural Affairs
DGV	Direct estimated Genomic Value
DYD	Average Daughter Yield Deviations
EAAP	European Association for Animal Production
EAS	Expression-Assisted Selection
EBV	Estimated Breeding Value
EDC	Effective Daughter Contribution
EGENES	Edinburgh Genetic Evaluations Services
EUBEEVAL	European International Beef Evaluation
GG	Genetical Genomics
G×E	Genotype by Environment interactions
GEBV	Genomically enhanced Estimated Breeding Value
GLM	General Linear Models
HY	Herd-Year
HYS	Herd-Year-Season
IBV	International Breeding Values
IC	Information Criterion
ICAR	International Committee for Animal Recording
ICBF	Irish Cattle Breeding Federation
IDF	International Dairy Federation
IE	l'Institut de l'Elevage
INRA	l'Institut National de la Recherche Agronomique
MACE	Multiple-Trait Across-Country Evaluation
MAS	Marker-Assisted Selection
MLC	the British Meat and Livestock Commission
NRS	Royal Dutch Cattle Syndicate
OECD	Organization for Economic Co-operation and Development
QTL	Quantitative Trait Loci
QTN	Quantitative Trait Nucleotide
REML	Restricted Maximum Likelihood
RMSE	Root Mean Square Error
SAC	Scottish Agricultural College
SNP	Single Nucleotide Polymorphism
Std	Standard Deviation
WGSL	Whole Genome Selection

Sammanfattning

Efter en Interbull workshop i Kuopio i juni 2006 togs beslutet att vidareutveckla ett system för en internationell avelsvärdering av köttrasdjur och i juni 2007 påbörjades ett treårigt projekt kallat Interbeef. Än så länge är deltagarländerna begränsade till Europa och den enda egenskapen som utvärderas är korrigerad avvänjningsvikt (vikt vid 200 dagar). Resultaten från en första internationell avelsvärdering har meddelats till länderna men är i dagsläget inte officiella. Avelsvärderingen baseras på data från renrasiga Charolais och Limousin. För att uppnå goda uppskattningar av avelsvärdena i ett internationellt sammanhang krävs det metoder för att kontrollera kvaliteten på indata och val av modell. I denna studie presenteras en metod A för att åstadkomma detta och som är framtagen specifikt för data från djur av köttras. Studien baserades på data från Sverige, Danmark, Storbritannien och Irland. Data från Frankrike kunde inte analyseras på grund av begränsad datorkapacitet. Metod A involverade beräkningar av Akaike's Information Criterion (AIC) för tre olika test modeller. En godkänd modell hade antingen lägst AIC, alternativt avvek den inte mer än 5 % från modellen med lägst AIC. De nationella modeller som analyserades i denna studie var av tillfredsställande kvalitet. Resultaten visade att korrelationer hade stor påverkan på värdet av AIC. Denna studie innehåller även en litteratursammanfattning av de nationella avelsvärderingarna som genomförs i Sverige, Danmark, Storbritannien (inklusive Nordirland), Irland samt Frankrike, inklusive det arbete som genomförs inom det genomiska området. Paralleller dras mellan de nationella avelsvärderingarna av köttrasdjur, den internationella avelsvärderingen av mjölkrasdjur och det arbete som utförs inom Interbeef på köttrasdjur.

Abstract

After a workshop in Kuopio held in June 2006, Interbull decided to go forward with the development of a system for beef international genetic evaluation and a three year project called Interbeef was launched in June 2007. The participating countries are so far limited to Europe and the only trait evaluated at present is adjusted weaning weight (weight at 200 days). The results from a first international genetic evaluation have been shared with the countries but are not yet official. The evaluation is based on data from purebred Charolais and Limousin. To achieve good estimates of proofs in an international context it is important that methods for data validation and model selection are implemented. Here a validation method A is suggested that have been specifically developed to suit beef data. This study was based on data from Sweden, Denmark, the United Kingdom (UK) and Ireland. The French dataset was not investigated due to limited computer capacity. Method A involved calculations of Akaike's Information Criterion (AIC) of three tests models. An approved model either had the lowest AIC value or differed no more than 5 % from the model with the lowest AIC. The models analyzed in this study were of adequate quality. The results also indicated that interactions had a large impact on the AIC. This study also includes a review of the national genetic evaluations, including research in the genomic area, performed in Sweden, Denmark, the UK, Ireland and France. Comparisons are made between the national genetic evaluations of beef cattle, the international genetic evaluation of dairy cattle and the work performed in Interbeef on beef cattle.

Introduction

The beef industry has gained a lot of attention lately. Due to the decreasing number of dairy farms and cattle that has been going on for some time and which has been reinforced by the present crisis in the dairy sector, countries which have traditionally relied on animals from the dairy sector to also cover a large proportion of the demand for beef, have seen a steady increase in the number of specialized beef cattle. An example is Sweden where the number of

suckler cows have increased from approximately 71 000 in the beginning of the 1980's to 186 000 in 2007 (Swedish Board of Agriculture, 2009a).

The Swedish population of specialized beef breeds is based on imports of genetic material as the country does not have any native beef breeds. In a paper by Eriksson *et al.* (2007), based on pedigree records from 1975 and onwards, it was shown that heavy beef breeds including Charolais, Limousin and Blonde d'Aquitaine have mainly been imported from France, Denmark and Canada. Within these breeds the number of French, Danish and Canadian sires with offspring in Sweden was found to be approximately 230, 160 and 110 respectively. Simmental, on the other hand, has mainly been imported from Germany followed by Canada, the Czech Republic and Denmark. The number of Simmental sires from Germany with offspring in Sweden was found to be close to 60 and the number of sires from the other countries close to 30. The Swedish populations of the smaller beef breeds Hereford, Aberdeen Angus and Highland cattle mainly originates from Canada, Great Britain, Denmark and the United States (US). Within these breeds the number of Canadian, British, Danish and American sires with offspring in Sweden was found to be approximately 180, 140, 70 and 60 respectively. A small proportion of both live animals and semen is exported from Sweden to countries mainly within Europe but also to the US and other countries within the Organization for Economic Co-operation and Development (OECD) (Hansson *et al.*, 2008).

The growing exchange of genetic material in both dairy and beef cattle is a global trend. In 2007 the international bull evaluation service (Interbull) had 42 member countries, which can be compared to 25 in 2001 (Canavesi *et al.*, 2001; Interbull, 2009a). Interbull is responsible for development and implementation of the international genetic evaluation of dairy cattle. It is a non-profit organization and a sub-committee of the International Committee for Animal Recording (ICAR) since 1988. The Interbull Centre is the coordinating body, situated in Uppsala, Sweden and provides the member countries with a number of services such as the international genetic evaluation service. The Interbull Centre is also a Community Reference Laboratory (CRL) for zootechnics and bovine breeding (Interbull, 2009a; Interbull, 2009b).

After a workshop in Kuopio held in June 2006, Interbull decided to go forward with the development of a system for beef international genetic evaluation. The Interbeef project started in June 2007 with the subscription of a three years project among the International Committee for Animal Recording (ICAR), Institute d'Elevage (IE, France), the Irish Cattle Breeding Federation (ICBF, Ireland), the Meat & Livestock Commission (MLC, United Kingdom) and the Nordic Cattle Genetic Evaluation (Denmark, Sweden and Norway). So far the participating countries in Interbeef are located only to Europe (Journaux *et al.*, 2006).

In an international genetic evaluation there are a number of issues that must be addressed, these include for example questions relating to genotype × environment (G×E) interactions, genetic linking or connectedness, data validation and model selection etc (Phocas *et al.*, 2005; Fouilloux *et al.*, 2006; Venot *et al.*, 2007; Venot *et al.*, 2008). G×E interactions are important as they may result in scaling or re-ranking of evaluated animals between different countries. These interactions may occur between most countries but appear to be stronger between the northern hemisphere and the Trans-Tasmanian block (including Australia and New Zealand) (Emanuelson *et al.*, 1999; Interbull, 2009a).

When it comes to data validation and model selection there exist a number of statistical tools to investigate model fit, or how well a model describes observations. There are also a number of software packages available to perform the statistical analyses, for example SAS, R and

SPSS. The SAS procedure General Linear Models (GLM) is used in uni- and multivariate analysis as well as regressions. In GLM the model fit is described by the determination coefficient R^2. For mixed models that include both fixed and random effects, the SAS procedure MIXED is a better method (Olsson & Engstrand, 2003). The statistical analyses in this study will be performed using the SAS procedure MIXED as the national models of the countries included in the study apart from being constructed differently contains both fixed and random effects. The MIXED procedure uses different information criterions (IC) including for example Akaike's Information Criterion (AIC), the Corrected Akaike Information Criterion (AICC), the Schwarz' Bayesian Information Criterion (BIC) and also the log likelihood of the Restricted Maximum Likelihood (REML) to investigate the model fit. These tools are not utilized in hypothesis testing, but rather in model selection (Olsson & Engstrand, 2003; SAS, 2009).

This study has two major aims. The first part consists of a literature review of the international genetic evaluation of dairy and beef cattle, the national genetic evaluation of beef cattle and progress within the area of genomic selection. Secondly a method for national data validation and model selection is developed by analyzing model fit using SAS procedure MIXED and different information criterions as well as the log likelihood. All statistical analyses are based on national data submitted to Interbeef by its participating countries.

Literature review

International genetic evaluation of dairy and beef cattle

Interbull and the international genetic evaluation of dairy sires

As mentioned Interbull performs the international genetic evaluation of dairy bulls. Interbull was initiated in the early 1980's as a collaboration between ICAR, the European Association for Animal Production (EAAP) and the International Dairy Federation (IDF). In 2007 Interbull had 42 member countries and the international genetic evaluation of dairy bulls included the following traits; production, conformation, udder health, direct longevity, calving traits, female fertility and workability (milking speed and temperament) (Interbull, 2009c). Data records and models used in the national genetic evaluations of these traits, in the member countries, are submitted to Interbull which perform a data validation followed by a Multiple-trait Across-Country Evaluation (MACE). Bulls to be included in the international genetic evaluation must have been progeny tested in at least one member country (Weigel & Rekaya, 2000; Interbull, 2009a).

Interbull performs three routine evaluations per year and two test evaluations. From the routine evaluations International Breeding Values (IBVs) are obtained and distributed to the member countries. Interbull does not rank the evaluated bulls, ranking and subsequent publication is performed by each national organization of the member countries. It is up to each country whether to publish the results or not. The test evaluations are performed to re-estimate genetic correlations between the participating countries, in this way changes in the evaluation systems of the countries and/or Interbull can be observed. International breeding values and genetic correlations obtained from the test runs are not published, but the national organizations are expected to verify the results (Interbull, 2009a).

Different methods have been suggested to produce an international proof, or IBV, from sire proofs originating from different countries. Schaeffer (1985) proposed a linear statistical model including additive genetic relationships. The model had the following design:

$$\mathbf{y} = \mathbf{Xc} + \mathbf{ZQg} + \mathbf{Zs} + \mathbf{e} \tag{I}$$

where
y = a vector of observed variable
X = incidence matrix related to the fixed effects (c)
c = a vector of fixed effects for country of proof
Z = corresponding incidence matrix for g and s
Q = a matrix that describes the group to which a sire belongs
g = a vector of fixed effects for country and year of birth of each bull
s = a vector of random sire effects, include a relationship matrix (A)
e = residual effects

The input data in the sire model I were national bull proofs (Schaeffer, 1994). In genetic studies by Rozzi *et al.* (1990) and Banos *et al.* (1991) model I was modified and deregressed bull proofs or approximated daughter averages were used as input instead. Analogous to deregressed bull proofs are average Daughter Yield Deviations (DYD). Daughter yield deviations can be defined as the lactation yield which has been adjusted for all fixed effects within a country such as management group, Herd-Year-Season (HYS), herd*sire, age and month of calving, as well as genetic merit of mates and cow permanent environmental effects (VanRaden & Wiggans, 1991; Schaeffer, 1994). To obtain conversion formulas DYD can be used in the MACE procedure (Schaeffer, 1994; Lidauer *et al.*, 2005). However, DYD varies within and across countries for all sires. The model has to manage this variability which constitutes a computational difficulty and therefore the total number of daughters per sire has been used as the dependent variable. This weighting factor ignores a number of effects that contribute to the variation in daughter information observed between sires and has been replaced by the Effective Daughter Contribution (EDC) in the present MACE procedure which is still based on a multiple-trait sire model. Effective daughter contribution including information from the dam alternatively EDC including information from all female ancestors take effects such as contemporary group, repeated records correlations and reliabilities of female ancestors into consideration (Fikse & Banos, 2001; Sullivan 2007).

Background Interbeef and international genetic evaluations of beef cattle

As for dairy cattle there is an increasing global exchange of beef genetic material. As a result there is also an increasing interest to be able to compare the national Breeding Values (BVs). Already in 1999 a research project was initiated with the aim to investigate a method for comparing BVs between different beef rearing systems as well as develop computer software for this purpose. Between 2001 and 2004 the Irish Cattle Breeding Federation (ICBF) in collaboration with ICAR, l'Institut National de la Recherche Agronomique (INRA, France), l'Institut de l'Elevage (IE, France), the British Meat and Livestock Commission (MLC, United Kingdom), the Australian University of New England (AGBU) and Interbull began developing the first European International Beef Evaluation (EUBEEVAL). The research indicated that a joint genetic evaluation for beef cattle was feasible, however, it was also found that there existed data quality issues that needed to be addressed (Journaux *et al.*, 2006; Venot *et al.*, 2007).

As mentioned the Interbeef project was launched at the beginning of 2007. France, Ireland, the United Kingdom, Denmark, Norway, Finland as well as Sweden all agreed on financial contributions and all countries, apart from Norway, are active participants of the Interbeef project. The results from a first international genetic evaluation have been shared with the

participating countries but not published officially. At present the international genetic evaluation of beef breeds is performed for purebred Charolais and Limousin, and only include the trait calf adjusted weaning weight (Journaux *et al.*, 2006; Venot *et al.*, 2007; Interbeef, 2009; Interbull, 2009a). In a survey performed by the Interbull Centre in 2009 the aim was to investigate what type of trait to be included next in the international genetic evaluation performed by Interbeef. The results indicate that the traits considered being of the most economical importance by most member countries are carcass weight and conformation as well as calving difficulty (Forabosco *et al.*, 2009a).

Possibilities of an international evaluation of beef cattle have been investigated in a number of studies also outside Europe. Issues that have been discussed include whether there exist significant genotype by environment (G×E) interactions as these may result in scaling or even re-ranking of evaluated animals between countries. As one of the aims of the international evaluation is to aid farmers and national breeding organizations/companies selecting sires from the global market, these interactions may have a large impact (Interbull, 2009a).

A joint genetic evaluation of beef cattle between Canada, the US and Uruguay has been suggested. In a study by de Mattos *et al.* (2000) G×E interactions for adjusted weaning weight in Herefords were investigated in different regions of the US as well as across the US, Canada and Uruguay. Data from Canada, Uruguay and US was composed of 487 661, 102 986 and 2 322 722 records on adjusted weaning weight respectively. It was shown that 359 sires had progeny in all countries. Estimates of genetic correlation for direct and maternal genetic effects for US – Canada, US – Uruguay and Canada – Uruguay were all between 0.8 and 0.9. This, according to earlier studies, indicates that no significant G×E interactions exist between these three countries (Robertson, 1959; Van Vleck & Cundiff, 1998). It was concluded that a joint genetic evaluation of weaning weight between the three countries could be possible and it was suggested that the model used in the evaluation should treat the data from the countries as a single population (de Mattos *et al.*, 2000).

Similar results were achieved in a study by Lee & Bertrand (2002) where G×E interactions for weaning weight in Herefords were investigated between Argentina, Canada, Uruguay and the US. Reports from Interbull also indicate that interactions are not as strong within the northern hemisphere or within the Trans-Tasmanian block as between the two blocks (Emanuelson *et al.*, 1999). In the international evaluation of dairy bulls G×E interactions are considered in the MACE procedure where each member country is treated as a separate environment or trait (Weigel & Rekaya, 2000; Interbull, 2009a).

An international genetic evaluation also requires that there exists sufficient genetic linkages across countries. This is mainly achieved through sires producing offspring in different countries. It is therefore necessary for each country participating in Interbeef to identify foreign animals utilized in the breeding population and their country of origin. A lot of genetic material from breeds such as Simmental, Montbéliard and Limousin has been exchanged particularly between the UK, Ireland and France. However, the flow of material is mainly from France to the British Islands and Ireland. Very little genetic material flows in the opposite direction, into France. In 2007 a new method for estimating the connectedness between countries was introduced in Interbull. The method is based on three principles where differences between genetic levels in different countries are simulated and percentages of the initial differences are measured using the Best Linear Unbiased Prediction (BLUP) methodology (Fouilloux *et al.*, 2006; Venot *et al.*, 2007; Venot *et al.*, 2008).

Another important issue to address is the choice of model in the international genetic evaluation. Phocas *et al.* (2005) analysed weaning weights from Limousin calves born in France and Australia/New Zealand. It was found that the model of choice in the international evaluation of beef cattle should be an animal model with raw data as input. The authors also questioned the feasibility of using MACE in the international evaluation of beef cattle as there may not exist sufficient genetic links across countries to achieve adequate estimates. It appears, so far, that the preferred model is a multiple trait animal model that includes a direct and a maternal genetic effects as well as a permanent environment dam effect (Phocas *et al.*, 2005; Venot *et al.*, 2007). Closely related to this issue is also the concern of data validation and national model selection.

Data validation

Validation of national data sets and the fit of genetic models is an important step in the international genetic evaluation. Integration of a quality management system in the genetic evaluation increases the quality of the estimated breeding values (EBVs) as well as results in more consistent estimates (Harbers, 2006). However, the level of quality depends to a great extent on how it is defined within the management system (de Jong, 1999).

All national data on dairy cattle submitted to Interbull must pass three trend validation tests. In method 1 evaluations of data from all lactations are compared to evaluations of only the first lactation. In this way it is possible to investigate any similarities between estimates of genetic trend. Method 2 has been developed to determine the stability over time of DYD. This is accomplished by analyzing the within-sire variation of DYD with consideration to calving year. While the first two models require access to raw data the third model is based on successive published evaluations of bulls. Method 3 has been designed to detect systematic trends as new information from additional daughters is added into the genetic evaluation. The assumption is that successive evaluations of any bull should be close to or equal to their true BV and that new information should only result in a random variation. To achieve adequate accuracy this method requires that evaluations have been performed during several years (Boichard *et al.*, 1995).

These methods can not be adopted into the international genetic evaluation of beef cattle for a number of reasons:

i) Method 1 and 2 require information on DYD, and as the raw data submitted to Interbeef is measured on males and females themselves and do not include lactations these methods are of no use in the evaluation of beef cattle.
ii) Method 3 is based on official predicted genetic merit. However, the national data sets submitted to Interbeef only contain raw data and not proofs of production traits or any other traits.
iii) All three methods are used to investigate genetic trends over time, this requires that evaluations have been performed during several years. At present, Interbeef have performed only one international evaluation and for this reason genetic trends can not be investigated. (Forabosco *et al.*, 2009b also see appendix 1)

Maximum likelihood and the information criterion

Different methods have been developed to investigate the model fit. The aim of the maximum likelihood principle, developed by R.A. Fisher during the 1920's, is to find a parameter vector *w* that will maximize the likelihood function *L(w/y)*. In the likelihood function the roles of the data vector *y* and parameter vector *w* in the original probability density function *f(y/w)* have

been reversed. In this way it is possible to find a probability distribution that best fit the observed data (Myung, 2003). In Restricted Maximum Likelihood (REML) the likelihood function has been partitioned into two parts. Where one part is free of fixed effects and following maximization REML estimators are obtained from this data set (Patterson & Thompson, 1971; Corbeil & Searle, 1976). The REML method is the preferred method when analyzing mixed models as it gives acceptable estimations of the variance components for both the fixed and random effects. The REML can also handle unbalanced data and the Satterthwaite-approximation (Olsson & Engstrand, 2003).

The maximum likelihood principle appears to be closely connected to information theoretic observations and a bias in the maximized log likelihood has been found to approximately correspond to the number of parameters included in the approximating model (Akaike 1973, 1974; Burnham & Anderson, 2004). An important concept in model selection is the statistical principle of parsimony and Occam's razor that encourage the use of the least complex model which still result in an adequate representation of observations. Having too few parameters in a model may increase the bias whereas too many parameters or over-parameterization may result in poor precision or identification of false effects (Forster, 2000; Burnham & Anderson, 2004). This has resulted in the formulation of Akaike's Information Criterion (AIC), where over-parameterization is penalized in the weighting of model complexity versus fit (Akaike 1973, 1974). The AIC is defined as:

$$\text{AIC}(\hat{\theta}) = (-2) \log(L) + 2k \tag{IIa}$$

$$\text{AIC} = n \log(\hat{\sigma}^2) + 2k \tag{IIb}$$

$$\hat{\sigma}^2 = \frac{\sum(\hat{\varepsilon}_i)^2}{n} \tag{IIc}$$

where
n = number of observations
$\hat{\varepsilon}_i$ = residuals from the model
k = number of parameters

The candidate models can then be ranked from worst to best depending on their AIC value, where a lower value is the better (Akaike, 1974; Burnham & Anderson, 2004). It is also important to note that the individual AIC values are much influenced by sample size (see equation IIb). The Corrected Akaike Information Criterion (AICC) converges into AIC as the sample size n increases. In practice this means that AICC should be used in first hand unless the sample size is large (Burnham & Anderson, 2004).

The Schwarz' Bayesian Information Criterion is defined as:

$$\text{BIC} = (-2) \ln(L) + k \log(n) \tag{III}$$

Schwarz' Bayesian Information Criterion (see equation III), though similar to AIC, is unrelated to information theory (Burnham & Anderson, 2004). Akaike (1973, 1974) suggests that the likelihood is maximized for each separate model whereas the BIC methodology is based on the use of priors (Schwarz, 1978). The BIC appears to introduce a rather large bias at

small sample sizes and is a better method in model selection at large sample sizes (Burnham & Anderson, 2004).

National genetic evaluation of beef cattle

France, Ireland, the UK, Denmark, Finland and Sweden are all active participants of the Interbeef project (Interbeef, 2009). For Sweden, Denmark, the UK, Ireland and France summaries of the national genetic evaluations are given below. Finland was excluded completely from this study as there was no data readily available from this country to perform the statistical analyses.

Sweden

In December 2007 the total number of suckler cows was 183 000. During the same period in 2008 this number had decreased to 181 036. Of the total number of cows in Sweden, the suckler cows constitute approximately 33 % (Swedish Board of Agriculture, 2009b).
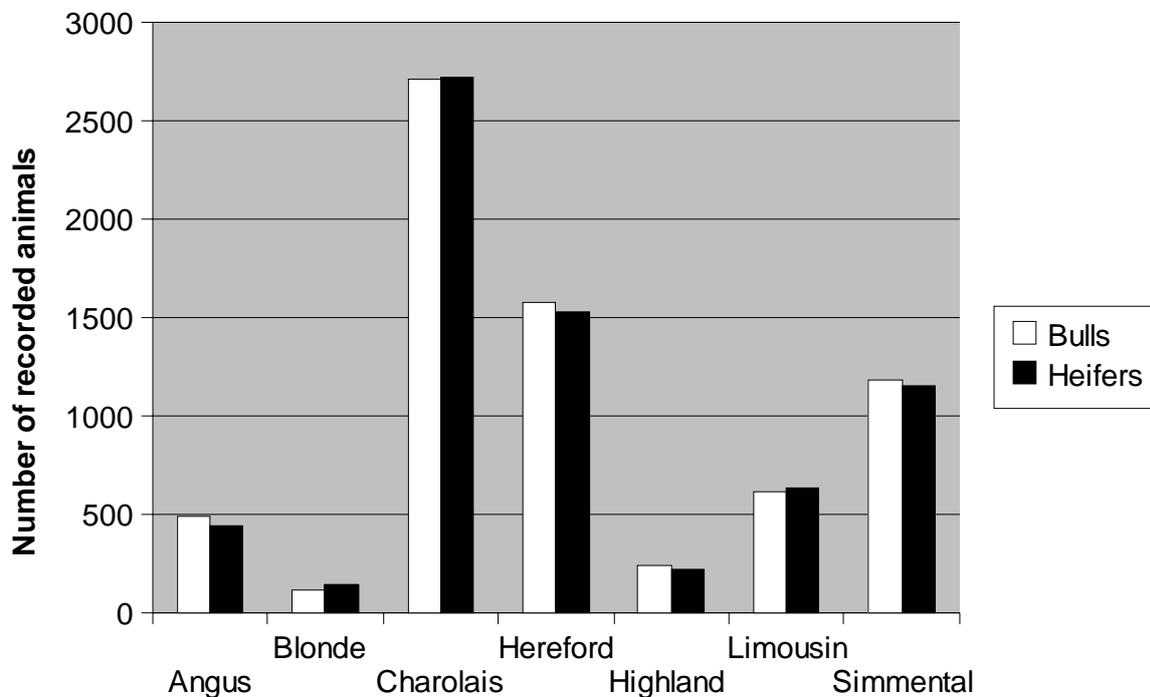
Figure 1. Number of calves recorded for birth weight in the Swedish official beef recording scheme 2008 grouped by sex and breed (Swedish Dairy Association, 2009).

During 2008 an average of 28 801 cows in 1 138 herds participated in the official beef recording scheme Kött Avel Produktion (KAP) run by the Swedish Dairy Association. During the same period the number of purebred calves born was 17 492, the number of calves with birth weight records was 14 090, 10 958 calves had weight records at 200 days (weaning weight) and 8 412 had records on yearling weight. The number of Charolais calves born equaled 6 401 and the number of Limousin calves equaled 1 348. In the case of Charolais 5 432 calves had birth weight records, 4 151 calves had weaning weight records and 3 195 had yearling weight records. For Limousin the corresponding number of calves with records was 1 247, 1 043 and 823 respectively. Figure 1 shows the number of bull and heifer calves in each breed with records on birth weight. Among the heavy beef breeds, Charolais dominates in the Swedish beef cattle population. Registration in KAP is only mandatory for active breeding herds (Swedish Dairy Association, 2009).

The breeding objectives of Swedish Charolais put emphasis on production traits such as growth, carcass traits and effective feed utilization. However, fertility traits, calvings, milk production, size and exterior as well as temperament are also considered. These are common breeding objectives within the Swedish beef cattle population including the Limousin breed (Swedish Charolais Association, 2009; Swedish Limousin Association, 2009).

The records used in the national genetic evaluation of Swedish beef cattle are collected from KAP as well as abattoirs, a bull station for performance testing and direct calving performances of dairy cows mated to beef sires (Eriksson *et al.*, 2007). Since 1993 the performance testing takes place at Gismestad bull station. The station has the capacity to test around 170 bulls per round. Bulls born between 31st of December and 31st of March are brought to the station during July. The bulls are given a few weeks to get acclimatized and the tests period begin in the end of August and continue until the end of January the following year. Data is collected on traits such as growth, health, fertility, conformation, feet and legs as well as temperament. The bulls are then ranked according to their growth given as a T-number. The T-number indicates an individual bull's growth relative that of the other bulls within the same breed and test year. Bulls with low T-numbers or that otherwise do not fulfill the minimum requirements with regards to health, fertility, conformation, feet and temperament are slaughtered. Bulls with T-numbers around the average are given back to the owners and may do well in commercial herds. The best bulls are termed elite bulls and are an important asset in the breeding work, especially in breeding herds. Bulls to be used in the Artificial Insemination (AI) program are selected from the elite bulls. Around 70 bulls receive adequate T-numbers to be sold at the beef breed auction which takes place in Linköping every year at the end of March (Avelspoolen, 2009; Svensk Köttrasprövning AB, 2009).

The Swedish breeding program relies to a large extent on records of purebred animals (Eriksson *et al.*, 2007). In 2000 the BLUP methodology was adopted in the genetic evaluation of beef cattle and at present BVs are estimated twice a year. The traits included in the genetic evaluation are birth weight (direct and maternal), daily gain from birth to 200 days (direct and maternal), daily gain from 200 days to 365 days, carcass traits (carcass fatness, fleshiness and net gain from birth to slaughter) and calving ability of first calvers (direct and maternal) (Swedish Dairy Association, 2000; Taurus, 2005).

In the evaluation of calving traits a multiple trait animal model is used. In the model birth weight and calving performance of first calvers are treated as different traits to those of older cows. The growth traits including birth weight are also evaluated in a multiple trait animal model. The evaluation of carcass traits is only performed for bulls (Eriksson *et al.*, 2007). As carcass traits are recorded on slaughtered animals the evaluation of bulls for these traits are mainly based on progeny results (Taurus, 2005). The carcass traits are evaluated simultaneously with the birth- and 200-day weight as suggested by Eriksson *et al.* (2003). The joint analysis of carcass and growth traits makes it possible to minimize bias due to selection. The evaluation results in three classes of BVs or sub-indices: a maternal index, a production index and an index for direct calving ease. In spring 2009 an integrated total merit index including these three sub-indices came into use (Eriksson *et al.*, 2003; Eriksson *et al.*, 2007; Näsholm, 2009).

Denmark

In 2008 an average of 106 000 cows were kept for suckling in Denmark and the number of farms with suckler cows was 8 922 (Statistics Denmark, 2009). In 2006, a total of 16 700 Limousine and 5 600 Charolais calves were born (Fogh, 2007).

The overall breeding objective in the Danish Limousin breed is the same as in all meat production, that is, to produce as much meat as possible while maintaining a minimal input of feed, work and capital. To achieve this emphasize is put on good carcass and beef characteristics as well as good mothering abilities. The calves also have to be viable with a good daily gain and effective feed utilization, but equally important is durable cows. Therefore the breeding objectives also include good conformation and fertility as well as good temperament (Danish Limousin, 2009). The breeding objectives for the Danish Charolais population are similar to those for Danish Limousine (Danish Charolais, 2009).

Since 1998 it is mandatory for active breeding herds as well as commercial herds to participate in the official recording. The traits included in the genetic evaluation are registered on both pure and crossbred animals, and are divided into the following groups: growth, birth, carcass quality, fertility, conformation. In the growth group the traits birth weight, weaning weight, yearling weight, carcass weight and body gain from performance testing are registered on purebred individuals. The only trait registered on crossbred animals is carcass weight. In the birth group birth weight, calving ease, survival at birth and at 200 days are recorded on purebred individuals, whereas only calving ease and survival at birth are registered on crossbred individuals. When it comes to carcass quality, carcass classification and the area of *Longissimus Dorsi* are registered on purebreds. In crossbreds only the carcass classification is registered. Fertility and conformation are only registered in purebred individuals. Fertility includes calving interval and conformation includes classification of body, muscling as well as feet and legs (Fogh, 2007).

The key organization in the national genetic evaluation is Dansk Kvæg (Interbeef, 2009). The EBVs are calculated separately for groups of breeds, where Limousin and Charolais belong to separate groups. The estimations are performed four times per year based on information from on-farm registrations, performance testing, conformation scoring and abattoirs (Fogh, 2007). Bulls are performance tested at the age 8 to 13 months. Data is collected and BVs estimated for the traits daily gain, area of *Longissimus Dorsi* and feed conversion efficiency. The feed consumption is recorded throughout the test period, whereas ultrasounds of the *Longissimus Dorsi* are performed at the ages 10, 11 and 12 months (Danish Cattle Federation, 2006).

The model used in the genetic evaluation of all traits recorded on purebred animals is a multiple trait animal model, which has been slightly modified in the case of crossbred animals. The BVs are presented in the form of a total merit index or S-index, which consist of a functional index and a production index. In total there are seven sub-indices: fertility, calving ability, milk production and birth make up the functional index. Weight gain and slaughter quality make up the production index. The last sub-index is conformation (Danish Cattle Federation, 2006; Fogh, 2007).

United Kingdom

In June 2008 the number of beef cows aged two years or older and having calved was approximately 1.4 million. This figure includes both purebred and crossbred animals. Cattle raised for beef make up the largest proportion (62.7 %) of the total cattle population in Great Britain (not including Northern Ireland) and most of these reside in Scotland. When

considering the total number of cattle the statistics show that 48 % of the farms keep between 1-50 heads and these make up 7 % of the cattle population in UK. About 3 % of the farms keep 500 heads or more which account for 21 % of all cattle in the UK (DEFRA, 2008).

The Limousin breed appears to be the most popular beef breed in UK. The breeding goals or quality charter include production of beef with a low percentage bone and fat, good carcass qualities, excellent productivity at low cost such as high food conversion, continuing excellence in cross breeding, good fertility and functional conformation as well as excellent mothering abilities including for example high milk production and easy calvings (British Limousin Cattle Society, 2009). The breeding objectives for the British Charolais population will not be investigated here.

The genetic evaluation of the British beef cattle population is performed by Edinburgh Genetic Evaluations Services (EGENES) in collaboration with the Scottish Agricultural College (SAC), the Roslin Institute and the University of Edinburgh. EGENES was established in 2004 to perform national genetic evaluations for dairy cattle. Since 2006 EGENES has also been commissioned by Signet to perform routine genetic evaluations for the British beef cattle population. Signet in turn is owned by MLC and is responsible for both beef cattle and sheep performance recording. The British Limousin Cattle Society in collaboration with the Suffolk Sheep Society and the British Texel Sheep Society are the founders of the Beef and Sheep Company (BASCO) database system. The genetic evaluation of beef cattle is based on data extracted from BASCO (Coffey et al., 2007).

The model used in the national genetic evaluation is a multiple trait animal model, which includes a fixed regression, maternal effects and permanent environmental effects of dam. Traits in the genetic evaluation are based on overall breeding objectives for all British beef breeds. These include the reproductive and functional traits calving difficulty, age at first calving, calving interval and longevity. The carcass quality indicators ultrasonic fat and muscle depth as well as muscle score evaluated at around 400 days of age are included in the carcass traits. Only two weight traits are included in the evaluation, these are weight at 200 and 400 days (Coffey et al., 2007; Interbeef, 2009).

The EBVs are combined into economic indices. The latest index to be added to the list was a Maternal Value index which includes the traits age at first calving, longevity, calving interval, maternal weaning weight and maternal calving ease. A total Maternal Production Value is then produced from the Maternal Value index, a Maternal Beef Value and a Calving Value (Coffey et al., 2007; Interbeef, 2009).

Ireland

During 2008 a total of approximately 1.6 million calves were sired by beef bulls. The Irish dairy and beef herds have a high interdependency and cross breeding is very common, both within and between dairy and beef breeds. About 50 % of the calves born to Friesian dams are sired by bulls of a breed other than Friesian, where the most common appears to be Aberdeen Angus. The same trend can be observed in beef breeds such as Limousin and Charolais where between 40 and 50 percent of calves born to a dam of these breeds are sired by a bull of a different breed (Department of Agriculture, Fisheries and Food, 2008). Concerning purebred animals, approximately 9 800 births were recorded in the breed society for Irish Limousin and 10 400 in the breed society for Irish Charolais (ICBF, 2008). Charolais bulls appear to be the preferred sires, independent of breed of the dam (Department of Agriculture, Fisheries and Food, 2008). The herd structure is similar to the UK (Evans et al., 2007).

The ICBF oversee the Irish beef cattle breeding activities. Animal records are kept in the ICBF database which is also integrated with the system for Calf registration and Animal Movement Monitoring (CMMS), now replaced by the Animal Identification and Movement (AIM) system (Evans *et al.*, 2007; Department of Agriculture, Fisheries and Food, 2008). The Irish Charolais Society in collaboration with the ICBF operate a new program for breed improvement called G€N€ IRELAND. Young bulls are selected within the program based on genetic indexes and linear scoring followed by performance testing at Tully. Older bulls are progeny tested for the economically important traits calving, weanling, slaughter and maternal value. Based on the outcome of the progeny test a number of bulls will become elite bulls. These will be included in the AI-program and will sire the next generation of stock bulls and replacement heifers (Irish Charolais Cattle Society, 2009a). The breeding objectives for the Irish Limousin are very similar to the French objectives for this breed. Emphasis is put on maternal qualities, especially milking ability, and beefing abilities including growth and muscle development. Emphasis is also put on better carcass conformation. Previously weak areas in the breed have been found to be growth rate and temperament. The French forecast is to improve the growth rate without increasing calving difficulties. Breeding for more docile animals have been successful (Irish Limousin Cattle Society, 2009).

A possible structure of the breeding objectives for the Irish beef cattle population was described by Amer *et al.* in 2001. The breeding objectives were divided into groups of traits: growth, weaned calf, calving, carcass and reproduction. The traits included in growth were direct weaning weight, feed intake summer/winter (though actual feed intake records are expected to be available only for selected individuals via performance testing), carcass weight and mortality. The weaned calf group included direct weaning weight and calf quality, calving included direct calving ease and direct gestation length. The carcass group included carcass fat and conformation score. The reproduction group included reproductive success, direct and maternal calving ease, direct and maternal weaning weight, annual/heifer and mature weight, as well as direct and maternal gestation length. Based on this information two total indices and six sib-indices where suggested. Later an overall suckler beef index was recommended as well as five sub-indices for calving performance, growth, weaned calf, carcass quality and reproductive efficiency. In 2005 the three sub-indices Calving Traits Index, Weanling Export Index and Beef Slaughter Index were introduced (Evans *et al.*, 2007).

Currently four genetic evaluations are performed to construct these indices. These are separated into a beef production evaluation, a calving performance evaluation, evaluation of maternal traits as well as an evaluation of maternal weaning weight. The goal traits in the beef production index include carcass weight, carcass conformation, carcass fat, weaning weight, cull cow weight, feed intake, calf quality, live weight and seven linear type traits. Calving difficulty (direct and maternal), gestation and mortality make up the calving performance index. The evaluation of maternal traits includes calving interval, survival and age at first calving. The evaluation of maternal weaning weight include the traits weaning weight, live weight and carcass weight. In addition an across breed evaluation is also performed by the ICBF, allowing comparisons to be made both within and across breeds. In the beef production evaluation a multiple trait across breed animal model is used and a similar model is used in the evaluation of maternal goal traits. The calving performance and maternal weaning weight evaluation is performed in ASREML using a multiple trait sire-maternal-grand sire model (Evans *et al.*, 2007).

Data on live weight and feed intake used in the genetic evaluation is collected at the Tully performance test station. Bulls entered at the test station are preselected by the ICBF in collaboration with the different breed societies. Selected bulls are inspected and those passing the inspection are given a health check. The bulls range in age from 7 to 12 months. The main traits of interest are feed conversion and growth efficiency. The information recorded at Tully is combined with information on weaning weight, calf value, linear scoring as well as slaughter information from abattoirs and pedigree information. The results are presented as €urostar indices. The ultimate goal of the performance testing is to select young bulls within G€N€ IRELAND that will eventually be eligible for progeny testing and later approved as AI bulls (ICBF, 2009).

France

In 2008 the total number of suckler cows in France was approximately 4.3 million. This number includes both purebred and crossbred animals. Beef replacement cows and heifers aged two years or older were approximately 970 000, whereas heifers in the same age group going to slaughter was close to 240 000. The number of bulls of beef breed was approximately 300 000 during the same period and in the same age group. In the age group one to two years the number of replacement heifers was 1.2 million, heifers sent to slaughter was close to 300 000 and the number of beef bulls 600 000 (Ministère de l'Alimentation, de l'Agriculture et de la pêche, 2009). In 2005 the number of recorded Charolais and Limousin cows was 317 972 and 186 005 respectively. Table 1 gives a brief summary of data included in the national genetic evaluation 2006 for Charolais and Limousin (Laloë *et al.*, 2007).

Table 1. Birth, growth and conformation traits for Charolais and Limousin in the French genetic evaluation 2006 (after Laloë *et al.*, 2007)

Breed	Trait	No. of evaluated animals	No. of records	No. of herds
Charolais	Birth	5 505 562	4 473 887	16 580
	Growth	3 162 617	2 528 553	8 146
	Conformation	3 215 882	2 601 308	7 805
Limousin	Birth	2 639 615	2 342 281	8 432
	Growth	1 861 873	1 666 714	5 544
	Conformation	1 620 685	1 430 408	5 006

The number of animals that are evaluated every year is extensive, in Charolais alone the number reached approximately 5.5 million individuals for the trait Birth (Table 1).

The selection objectives within French Charolais put emphasis on traits such as fertility, easy calvings, milk production, hardiness, feet health, growth and development capacity as well as carcass conformation among other (Herd Book Charolais, 2009). These objectives show great similarities with those within the French Limousin, where emphasis also is put on fertility, health, feed conversion etc (La Limousine, 2009).

In 1991 the BLUP animal model was adopted in the French genetic evaluation. Since 1994 IBOVAL is the official evaluation and include nine breeds of beef cattle, from France, Italy, Luxemburg, Spain and the Netherland. The national genetic evaluations are run by INRA in collaboration with IE. Data is extracted from a national database which contains information from on-farm registrations of calving ease score, weights at birth, 120 days and 210 days as well as linear scores for muscular, skeletal and functional abilities around weaning. Further,

the database also contains information on carcass traits collected from abattoirs (Laloë *et al.*, 2007).

The evaluations are performed separately for each breed, based on the breed of the dam, and are mainly performed for purebred animals. The two exceptions are the Salers and Aubrac breeds where the genetic evaluations also include calves sired by Charolais bulls. At present four evaluations are performed in France: the calving performance evaluation, the growth evaluation, the conformation at weaning evaluation and the carcass evaluation. The calving performance evaluation include the traits calving ease and birth weight and is based on a multiple (two) trait animal model. The only trait included in the growth performance evaluation for the Charolais and Parthenaise is 210-day adjusted weaning weight. This trait is evaluated using a single trait animal model which includes maternal effects. For the other breeds a multiple (two) trait animal model is used and the traits evaluated include both 120-day and 210-day weight. In the conformation at weaning evaluation muscular and skeletal developments are evaluated simultaneously in a two trait animal model. The linear scores are evaluated separately in a single trait animal model. None of the models take maternal effects into consideration. Carcass weights, EUROPA muscular scores and slaughter age of bulls are evaluated jointly in a multiple trait animal model with weaning weight, including maternal effects, and weaning muscling score. The carcass evaluation includes all animals that also have results from the growth and conformation evaluations up to weaning (Laloë *et al.*, 2007).

From the EBVs received from these evaluations three total merit indices are produced. One of these combine the direct effects of the separate traits, the second is a maternal weaning index where both direct and maternal effects are combined and the last index includes the carcass traits. Future work includes among other things to develop the genetic evaluation to allow the inclusion of crossbred animals and also to consider maternal fertility and productivity (Laloë *et al.*, 2007).

Genomic selection

Traditionally, the genetic evaluation has been based solely on phenotypic records. As the molecular genetic techniques have greatly improved and bovine linkage maps are now available, an additional strategy could be to identify and select animals based on DNA-marker haplotypes coupled to economically interesting production traits such as milk or beef traits etc. So called Marker-Assisted Selection (MAS) is facilitated by the existence of major genes or Quantitative Trait Loci (QTL) controlling these traits (Sonstegard & Gasbarre, 2001; Sonstegard & Van Tassell, 2004) and would reduce the need of progeny testing which would greatly increase the rate of genetic gain. Rate of gain is given by:

$$\Delta G = \frac{i * r * \sigma_a}{L} \qquad \text{(IV)}$$

where
ΔG = rate of genetic gain per year
i = selection intensity
r = accuracy of estimated breeding value (selection)
σ_a = standard deviation of additive genetic variation in the population
L = average generation interval

It is intuitive that genomic selection will affect most components in equation IV. As genomic selection reduces the need for progeny testing the generation interval may be reduced,

especially if genomic selection is used together with appropriate reproductive techniques. Genomic selection also has the potential to increase the selection intensity and accuracy of EBVs (Kadarmideen *et al.*, 2006). Schaeffer (2006) investigated the advantages of genome wide selection as well as the possibilities to modify or replace traditional progeny testing and the effect this would have on the rate of genetic gain and economics in livestock breeding. The effect on predicted genetic change in traditional progeny testing is compared to using a genome wide strategy in Table 2.

Table 2. Four pathways of selection in progeny testing and genome wide selection (after Schaeffer, 2006)

Pathway	Selection, %	Progeny testing			Genome wide selection		
		i	r	L	i	r	L
Sire of bulls	5	2.06	0.99	6.5	2.06	0.75	1.75
Sire of dams	20	1.40	0.75	6	1.40	0.75	1.75
Dams of bulls	2	2.42	0.60	5	2.42	0.75	2
Dams of cows	85	0.27	0.50	4.25	0.27	0.50	4.25
Total				21.75			9.75

Similar values of selection intensities (i), accuracies (r) and generation intervals (L) as those shown in Table 2 have been presented by Schmidt & Van Vleck (1974), Bourdon (2000) and Van Doormaal & Kistemaker (2003). The values are based on a trait with a heritability of approximately 0.4. By summing up the products i*r for each pathway, Schaeffer (2006) showed that progeny testing resulted in 4.68 genetic standard deviations and 21.75 years which would give a genetic standard deviation change per year equal to 0.215. This can be compared to genome wide selection which would, following the same reasoning, result in 4.55 genetic standard deviations and 9.75 years which would give a genetic standard deviation change per year equal to 0.467. The calculations performed by Schaeffer (2006) showed that genome wide selection resulted in a change of the genetic standard deviation per year which was twice that of the rate of change in progeny testing. Table 1 also show that the greatest gain in the rate of genetic change was achieved through the dam of bull pathway.

The study was based on a trait with a heritability of 0.4. It is possible that the response in genetic gain may be even greater for low heritability traits, such as health and fertility traits, where traditional progeny testing require a great number of observations to give adequate accuracies which also will prolong the generation interval.

In a study by Meuwissen *et al.* (2001) the effects of ~50 000 marker haplotypes were investigated in a simulated population. In the first 1 000 simulated generations the effective population size was $N_e = 100$. This was increased to $N_e = 200$ in generation 1 001 and $N_e = 2 000$ in generations 1 002 and 1 003. Animals in the 1 001 and 1 002 generations received phenotypic records and were also genotyped for a certain trait. Animals in the 1 003 generation were assumed to be too young to have received phenotypic records and therefore estimates of their BVs were based exclusively on marker information. Predictions of the genetic merit in the 1 003 generation were made using least-squares, BLUP and Bayesian analyses. The results from the different analyses were then compared based on the accuracy of the predications. Least-squares appeared to be the least reliable method for predicting the genetic merit of the offspring. However, with the least-squares method it was not possible to estimate all haplotype effects simultaneously. The accuracy was only 0.32 when the greatest

effects were included and effects were overestimated. A higher accuracy of 0.73 was obtained using BLUP, but on the other hand this method required some assumptions of the variance associated with the chromosomal segments that may not be realistic. The main problem with BLUP, however, appeared to be the regression back to zero of large QTLs. With the Bayesian method the accuracy was increased to 0.85. The authors concluded that genomic selection may be feasible to increase genetic gain in livestock production.

In a review by Sellner *et al.* (2007) the slow progress in the identification of economically important QTLs and Quantitative Trait Nucleotides (QTN) in livestock was attributed to bad population designs, slow fine-mapping and an inability to detect candidate QTNs. The authors discussed emerging technologies such as for example high-throughput Single Nucleotide Polymorphism (SNP) genotyping assays and their application in livestock to increase the genetic merit and improve management. It was suggested that the marker-based method known as Whole Genome Selection (WGSL), described by Meuwissen *et al.* (2001), would be of greater benefit than for example Genetical Genomics (GG) and Expression-Assisted Selection (EAS) described by Kadarmideen *et al.* (2006). Genetical genomics is a system genetics approach that combines transcriptomics and pathway data with QTL mapping. Sellner *et al.* (2007) also emphasized that the full benefit of WGSL was most likely to be apparent in systems based on selection indices rather than single trait BVs. Genetical genomic selection indices were also suggested in the review by Kadarmideen *et al.* (2006).

In view of the fast progress occurring within the genomic research, Interbull appointed a task force with the main objectives to develop a "scientific framework for the use of genomic data in national and international genetic evaluations" as well as to promote international collaboration (Banos *et al.*, 2009). First a standardization of terminology was recommended. Conventional EBVs do not include genomic information, whereas a Direct estimated Genomic Value (DGV) is based solely on genomic information. By combining EBV and DGV a Genomically enhanced Estimated Breeding Value (GEBV) is obtained. Then, depending on the type of genomic information that will be available at Interbull, different methodologies have to be developed and implemented in the international genetic evaluation. Five possible scenarios have been investigated. If Interbull have access to both national EBVs and bull genotypes it would be possible to set up an international genotype database. This would allow the Interbull Centre to perform its own SNP genotyping assays something that especially would benefit small populations where the national data is insufficient to allow accurate SNP estimates. In another scenario Interbull may have access to national EBVs, bull genotypes and SNP national prediction equations which would significantly facilitate the operational flow as the Interbull Centre would not need to estimate the SNP effects. Assuming a third and fourth scenario where Interbull only have access to national EBVs and DGVs alternatively national EBVs and GEBVs the question becomes how to combine and incorporate these into the international genetic evaluation. On the other hand, if Interbull only has access to national GEBVs this may affect the conventional international genetic evaluation negatively. It would only be possible to estimate MACE GEBVs and no MACE EBVS would be available for estimating SNP effects. The most desirable situation is where it would be possible to combine and incorporate national EBVs, DGVs and GEBVs into the international genetic evaluation as well as setting up an international bull genotype database.

As mentioned above G×E interactions are of great importance in the international genetic evaluation of livestock. Using the GG approach it may be possible to identify interacting environment specific QTLs. According to Kadarmideen *et al.* (2006) this could make it possible to weight the importance of genes which in the end would result in more appropriate

decisions with regards to animal breeding. More pathways would open up and it would no longer be necessary to choose between breeding for more generalized or more specialized animals. With GG it would be possible to have a more directed and specific breeding scheme depending on the situation. An issue that must not be forgotten is the risk of an increased rate of inbreeding, which must be addressed in all breeding programmes.

In Ireland genomic selection has already been incorporated into the national breeding programme for dairy cattle and its current status is investigated in a paper by Berry *et al.* (2009). Out of 54 001 SNPs originally available, 42 598 were included in the analysis. Sires that failed parentage testing were removed, leaving 1 209 Holstein-Friesian bulls available. In the Irish genomic evaluation the dependent variable is the individual's EBV. The increase in reliability for GEBVs was found to be relatively small (0.01 for locomotion and 0.18 for fertility) compared to for example the US. In a study from the US by VanRaden *et al.* (2009) the realized reliabilities were found to be approximately 23 % greater than those of parent averages (averaged over all traits).

The New Zealand dairy sector GEBVs have been computed in a similar way as the Irish. The two technologies used in New Zealand are Customized CRV Illumina 60K and Illumina Bovine SNP50 BeadChip, and 44 146 SNPs have been utilized in the analyses (Harris & Montgomerie, 2009). The New Zealand GEBVs have also been found to have a greater reliability than the Irish GEBVs. It has been suggested that the reason behind the low Irish reliabilities is most likely the small training population size. To improve the reliabilities Ireland have begun to investigate the possibilities for an across-country genomic evaluation in collaboration with New Zealand (Berry *et al.*, 2009).

In a genomic study on data from Swedish and Danish Holstein it was concluded that there exists a sufficient base for genomic selection in these populations. The average reliability of the GEBVs for 17 different traits was found to be 0.513, or moderately high. This figure was found to be twice that of parentage average reliability and based on these results the breeding company VikingGenetics has begun to pre-select young Danish Holstein bulls for progeny test based on their GEBVs (Lund & Su, 2009). At present Sweden, Denmark and Finland all use genomic information to select future elite dairy bulls. A BV including genomic information has been developed in a Nordic collaboration on genomic selection and this BV is planned to be implemented in the end of 2009 (VikingGenetics, 2009). The beef sector is lagging somewhat behind in this area and the incorporation of genomic information in the Nordic genetic evaluations of beef cattle still lies in the future.

The possibility of using genomic information in the British genetic evaluation of beef cattle is being investigated and collection of genomic information has begun (pers. comm. Forabosco, 2009c). As mentioned above, genomic selection has already been incorporated into the national genetic evaluation of Irish dairy cattle (Berry *et al.*, 2009; Loberg & Dürr, 2009) and its application in the beef sector is being investigated. In France MAS has been incorporated in the national genetic evaluation since 2001 for the dairy breeds Holstein, Montbéliarde and Normande. Since 2008 a large number of animals of dairy breeds have been genotyped to be used in SNP genotyping assays. A recently started research project, Amasgen (Methodology and Application of Genomic Selection), aims among other things to develop prediction equations using a genomic approach as well as to develop a validation method (Ducrocq *et al.*, 2009; Loberg & Dürr, 2009). The use of genomic information in the genetic evaluation of beef cattle is also being investigated and France like UK has begun genotyping animals (pers. comm. Forabosco, 2009).

Concerning the role of Interbull there seems to exist four distinct questions at issue:

i) Continuation of the traditional international genetic evaluation without the inclusion of genomic information.
ii) Provision of international GEBVs.
iii) Aiding in the exchange of genomic information and strategies/methodologies utilized in the genomic selection.
iv) Ensuring the quality control by setting standards and implementing validation methods. (Banos *et al.*, 2009; Loberg & Dürr, 2009).

Performed Study

Material and Methods

National Data and Models

In this study datasets submitted to Interbeef from Sweden, Denmark, the UK and Ireland on the traits unadjusted as well as adjusted weaning weight (the weight is adjusted to weight at 200 days), have been analyzed (Table 3). The datasets contain information for two breeds of beef cattle, namely Charolais and Limousin. Both males and females are included in the study. France was excluded due to a too large dataset and limited computer capacity.

Table 3. Datasets utilized in the analyses

Country	Breed	No. of obs.	Obs. years	Criteria for inclusion of records in national genetic evaluation
Sweden (SWE)	Charolais	91 200	1986 to 2008	Recorded birth weight, known sire and dam and only purebred (88%) animals
	Limousin	16 467	1987 to 2008	
Denmark (DEN)	Charolais	13 977	1983 to 2008	The minimum weight for inclusion is 50 kg and the maximum weight is 600 kg. Animals moved from a herd during the period of birth to time of weighing are excluded.
	Limousin	35 104	1980 to 2008	
United Kingdom (UK)	Limousin	99 262	1972 to 2007	The maximum weight range for inclusion is 500 kg. The acceptable age range for weighing is between 170 and 300 days.
Ireland (IRE)	Charolais	14 054	1974 to 2008	-3Std =< breed*sex mean =< +3Std
	Limousin	8 777	1975 to 2008	

Sweden

The Swedish dataset contains information on weaning weight from 91 200 Charolais and 16 467 Limousin purebred animals. An animal is considered purebred as long as crossbreeding does not exceed 12 % (Table 3). Adjusted weaning weight is defined as the weight at 200 days. Recordings are performed between 150 and 250 days of age by the farmer under supervision of assistants from the Swedish Dairy Association, the official Swedish

recording organization, using scales. The model used in the national genetic evaluation and submitted to Interbeef is a multiple trait animal model including maternal effects. The national model includes the following environmental effects: HYS, sex, season, age of dam and multiple births. All environmental effects are treated as fixed effects. In the original model the fixed effects HYS and sex are only included as an interaction HYS*sex (Interbeef, 2009).

Denmark

The Danish dataset contains information on unadjusted and adjusted weaning weight from 13 977 Charolais and 35 104 Limousin cattle (Table 3). Adjusted weaning weight is defined as the weight at 200 days. Recordings are performed between 140 and 260 days of age by the farmer using scales. To evaluate these recordings technicians weigh sample herds. The model used in the national genetic evaluation and submitted to Interbeef is a multiple trait animal model including maternal effects. The model includes the following environmental effects: herd-year (HY), season of calving, sex and twinning. In the model the interactions age at weighing*sex and age of dam*parity are also considered. All these environmental effects are treated as fixed effects. In addition the following random effects are also included in the national model: permanent environment of the dam, maternal and direct (calf) effects (Interbeef, 2009).

In addition the data files on unadjusted weaning weight also contained information regarding the fixed effect of average age at weighing.

United Kingdom

The British dataset contains information on weaning weight from 99 262 Limousin cattle. There is no information available from the Charolais breed (Table 3). Adjusted weaning weight is defined as the weight at 200 days. Recordings are performed between 170 and 300 days of age by the breeders on farm using scales. The model used in the national genetic evaluation and submitted to Interbeef is a multiple trait animal model, in which a fixed regression, maternal effects and maternal permanent environmental effects are considered. The model includes the following fixed environmental effects: HY, birth month, sex, foster code, birth type and age of dam. The age of the dam is treated as a regression with a linear and quadratic effect (Interbeef, 2009).

Ireland

The Irish dataset contains information on weaning weight from 14 054 Charolais and 8 777 Limousin cattle (Table 3). Adjusted weaning weight is defined as the weight at 200 days. Recordings are performed between 150 and 300 days of age on farm, by linear scorers and at marts/markets using scales. The model used in the national genetic evaluation and submitted to Interbeef is a multiple trait animal model which includes the following fixed environmental effects: HYS, HYS for previous herd, sex, age at weighing and parity of dam. In the model the interactions sex*age at weighing, sex*age at weighing*age and sex*age at weighing*age*age are considered as well as random effects due to heterosis and recombination in the case of crossbred animals (Interbeef, 2009).

Data submitted to Interbeef on adjusted weaning weight only included the effects of HYS and sex. Data on unadjusted weaning weight also included information on first age at weighing, average age at weighing and average weight. This extra information allowed the inclusion of the fixed effect average age at weighing and the interaction sex*age at weighing.

Statistical analysis

Due to the nature of this study it was necessary to simplify the models referred to as the national models. Due to limited computoral capacity (or insufficient temporary memory space) pedigree information was not included and random maternal effects were not analyzed. As weaning weight is only registered once per animal, random calf (direct) effects were also excluded. Random effects due to heterosis and recombination were also excluded as no crossbred animals were included in this study. The fixed effects of the national models were analyzed using SAS mixed models procedures (SAS, 2009). The model was set up as a single trait animal model, adjusted and unadjusted weaning weight were analyzed separately.

Below is an example of a SAS program that was used for analyzing adjusted weaning weight in Danish Charolais (see description of national model in Material and Methods):

```
title 'Test 1 – The original model';
proc MIXED data=cousl4 ic METHOD=REML;
   class hy ef1 ef2 ef3 ef4 ef5;
   model adww=hy ef1 ef2 ef3 ef4 ef5;
run;
quit;
```

where
cousl4 = input file
hy = contemporary group (herd *year)
ef1 = season of calving
ef2 = age of dam*parity
ef3 = sex
ef4 = twin
ef5 = age at weighing*sex

To investigate the fit of model REML, AIC, AICC and BIC was used. For each country and breed combination three test models were set up and AIC, AICC, BIC and -2 res log likelihood were calculated for each model. Test model 1 was the adjusted national model, model 2 and 3 were generated by including interactions or excluding certain effects. Effects included in generated interactions were no longer included as main effects. Based on the AIC values within a testbattery consisting of three test models generated for each country and breed combination a Standard Deviation (Std) was calculated. For a test model to be approved the AIC of the model was not allowed to pass an upper limit. The upper limit was calculated as the lowest AIC within the test battery + 1 Std and + 5 %.

Results

Sweden and Denmark

The number of animals had to be reduced when the Charolais files were analyzed as the memory space was limited. This was done by sorting the animals randomly and choosing the first 70 000 for the analyses. The results of the analyses of the Swedish data on adjusted weaning weight are summarized in Table 4.

The values were the same for AIC and AICC as well as for BIC and -2 res log likelihood. The differences between AIC/AICC and BIC/-2 res log likelihood were very small. In both Charolais and Limousin the model with the smallest IC and -2 res log likelihood was the

adjusted national model. The Std in Swedish Charolais was 21 160. As model 1 had the smallest AIC value of 615 406 this resulted in maximum AIC of: 615 406 + 21 160 = 636 566 and 615 406 + 5 % = 646 176. Test models with AIC values exceeding maximum AIC will not be approved. In this case only test model 1 was approved. The Std in Swedish Limousin was in turn 5 220. As model 1 had the smallest AIC value of 132 184 this resulted in maximum AIC of: 132 184 + 5 220 = 137 404 and 132 184 + 5 % = 138 793. Again, only model 1 was approved (Table 4).

The effect of sex was divided into four categories in the original Danish files, sex 1 and 3 were males, sex 2 and 4 were females. The number of animals recorded with sexes three or four constituted approximately 4 % of the total number of animals. They were considered to be recording errors and were excluded from the analysis. The number of Danish Charolais included in the analysis were in total 13 449 after the corrections. The same procedure was performed for the Danish Limousin and after the corrections the number of observations left for analysis was 34 686. However, after exclusion of animals with sexes three and four the remaining number of animals to be included in the analysis had to be reduced further in the case of adjusted weaning weight, due to limited memory space. This was done by sorting the animals randomly and the final number of Danish Limousin animals included in the study was 20 000 (Table 5, 6).

The significance of sex when included as a main effect in test model 1 and 2 on adjusted weaning weight, for both breeds, was not calculated due to zero degrees of freedom which was due to the fact that sex was also included as an interaction with age at weighing. The interaction was of the same significance as the other effects ($p < 0.001$). In test model 3 sex had the same significance as the other effects included in the model for Danish Charolais but was not significant in the case of Limousin ($p = 0.6548$) (Table 5).

The values were the same for AIC and AICC as well as for BIC and -2 res log likelihood in the Danish dataset on adjusted weaning weight. The differences between AIC/AICC and BIC/-2 res log likelihood were very small. In both Danish Charolais and Limousin the model with the smallest IC and -2 res log likelihood was model 2 which included an interaction between HY and season of calving .The Std in Danish Charolais was 20 328. As model 2 had the smallest AIC value of 78 089 this resulted in maximum AIC of: 78 089 + 20 328 = 98 417 and 78 089 + 5 % = 81 993. In this case, test model 1 was not approved. The Std in Danish Limousin was 27 995. As model 2 had the smallest AIC value of 114 862 this resulted in maximum AIC of: 114 862 + 27 995 = 142 857 and 114 862 + 5 % = 120 605. As for Charolais test model 1 was not approved (Table 5).

The additional effect of age at weighing was not included in the analyses on unadjusted weaning weight as a main effect as it was already included as an interaction age at weighing*sex. As for adjusted weaning weight sex had zero degrees of freedom (Table 6).

The values are the same for AIC and AICC as well as for BIC and -2 res log likelihood and the differences between AIC/AICC and BIC/-2 res log likelihood are very small same as for adjusted weaning weight. In both Danish Charolais and Limousin the model with the smallest IC and -2 res log likelihood is the adjusted national model 1. The Std in Danish Charolais was 778. As model 1 had the smallest AIC value of 115 089 this resulted in maximum AIC of: 115 089 + 778 = 115 867 and 115 089 + 5 % = 120 844. In this case, + 1 Std will cause only model 1 to be approved, whereas + 5 % will cause all three models to be approved of. The Std deviation in Danish Limousin was 1 396. As model 1 had the smallest AIC value of 286 406

this resulted in maximum AIC of: 286 406 + 1 396 = 287 802 and 286 406 + 5 % = 300 726. In this case, + 1 Std will cause only model 1 to be approved, whereas + 5 % will cause all three models to be approved of (Table 6).

Table 4. Swedish test models for adjusted weaning weight, significance of fixed effects and values of AIC, AICC, BIC and -2 res log likelihood for each test model as well as maximum AIC calculated as + 1 Std and + 5% from the test model with the smallest AIC value

Breed	No. of observations Original data	Analyzed data	Model	Significance of fixed effects	AIC	AICC	BIC	-2 res log likelihood	AIC + 1 Std	AIC + 5 %	Approved / Not app.
Charolais	91 200	70 000[d]	1[a]	***	615 406	615 406	615 402	615 402	636 566	646 176	App.
		70 000	2[b]	***	647 303	647 303	647 301	647 301			Not app.
		70 000	3[c]	***	655 440	655 440	655 438	655 438			Not app.
Limousin	16 467	16 467	1[a]	***	132 184	132 184	132 182	132 182	137 404	138 793	App.
		16 467	2[b]	***	141 326	141 326	141 324	141 324			Not app.
		16 467	3[c]	***	141 381	141 381	141 379	141 379			Not app.

[a] Adjusted national model as described in Material and Methods.
[b] The interaction HYS*sex was excluded.
[c] The interaction HYS*sex and the effect of season of calving were excluded.
[d] The number of animals had to be reduced as the memory space was limited.
*** All fixed effects were significant ($p < 0.001$).

Table 5. Danish test models for adjusted weaning weight, significance of environmental effects and values of AIC, AICC, BIC and -2 res log likelihood for each test model as well as maximum AIC calculated as + 1 Std and + 5% from the test model with the smallest AIC value

Breed	No. of observations Original data	Analyzed data	Model	Significance of fixed effects	AIC	AICC	BIC	-2 res log likelihood	AIC + 1 Std	AIC + 5 %	Approved / Not app.
Charolais	13 977	13 449[d]	1[a]	***	113 370	113 370	113 366	113 366			Not app.
		13 449	2[b]	***	78 089	78 089	78 085	78 085	98 417	81 993	App.
		13 449	3[c]	***	78 233	78 233	78 229	78 229			App.
Limousin	35 104	20 000[e]	1[a]	***	163 505	163 505	163 501	163 501			Not app.
		20 000	2[b]	***	114 862	114 862	114 858	114 858	142 857	120 605	App.
		20 000	3[c]	***	115 171	115 171	115 167	115 167			App.

[a] Adjusted national model as described in Material and Methods.
[b] An interaction HY*season of calving was included.
[c] The interaction HY*season of calving was retained and the effect of age at weighing*sex was excluded.
[d] Animals were excluded due to errors in recording of sex.

*** Fixed effects were significant (p < 0.001).

Table 6. Danish test models for unadjusted weaning weight, significance of environmental effects and values of AIC, AICC, BIC and -2 res log likelihood for each test model as well as maximum AIC calculated as + 1 Std and + 5% from the test model with the smallest AIC value

Breed	No. of observations		Model	Significance of fixed effects	AIC	AICC	BIC	-2 res log likelihood	AIC + 1 Std	AIC + 5 %	Approved / Not app.
	Original data	Analyzed data									
Charolais	13 977	13 449[d]	1[a]	***	115 089	115 089	115 085	115 085	115 867	120 844	App.
		13 449	2[b]	***	116 295	116 295	116 291	116 291			App.
		13 449	3[c]	***	116 544	116 544	116 540	116 540			App.
Limousin	35 104	34 686[d]	1[a]	***	286 406	286 406	286 402	286 402	287 802	300 726	App.
		34 686	2[b]	***	288 375	288 375	288 371	288 371			App.
		34 686	3[c]	***	289 105	289 105	289 101	289 101			App.

a) Adjusted national model as described in Material and Methods.
a) The effects of age of dam*parity and twinning were excluded.
c) The effect of age of dam*parity, twinning and season of calving were excluded.
d) Animals were excluded due to errors in recording of sex.
*** Fixed effects were significant (p < 0.001).

United Kingdom and Ireland

The number animals had to be reduced as the memory space was limited. This was performed in the same way as for Swedish Charolais and Danish Limousin by sorting the animals randomly and choosing the first 30 000 for the analyses. In the file submitted to Interbeef there was no information on the fixed effect foster code.

The values were the same for AIC and AICC as well as for BIC and -2 res log likelihood in the British dataset. The differences between AIC/AICC and BIC/-2 res log likelihood were very small. Model 3 which included an interaction received the smallest AIC value. The Std in British Limousin was 35 311. As model 3 had the smallest AIC value of 201 623 this resulted in maximum AIC of: 201 623 + 35 311 = 236 934 and 201 623 + 5 % = 211 704. In this case, only test model 3 was approved (Table 7).

The Irish data submitted to Interbeef was incomplete and a lot of information regarding the fixed effects included in the national model as described in the Interbeef form (Interbeef, 2009) was missing. The data file only included the fixed effects HYS and sex. In the case of unadjusted weaning weight there was also information on the fixed effect average age at weighing.

When unadjusted weaning weight was analyzed the fixed effects sex and age at weighing were included both as main effects and an interaction which affected the significance of the included effects as described in Table 9.

In case of both adjusted and unadjusted weaning weight the values were the same for AIC and AICC as well as for BIC and -2 res log likelihood in the Irish dataset. The differences between AIC/AICC and BIC/-2 res log likelihood were very small (Table 8, 9). In both Irish Charolais and Limousin the model for adjusted weaning weight with the smallest IC and -2 res log likelihood was model 2 (Table 8) whereas it was model 1 for unadjusted weaning weight (Table 9).

For adjusted weaning weight the Std in Irish Charolais was 8 528. As model 2 had the smallest AIC value of 112 041 this resulted in maximum AIC of: 112 041 + 8 528 = 120 569 and 112 041 + 5 % = 117 643. Test model 2 was the only approved model. The Std in Irish Limousin was 6 541. As model 2 had the smallest AIC value of 61 660 this resulted in maximum AIC of: 61 660 + 6 541 = 68 201 and 61 660 + 5 % = 64 743. Again, only test model 2 was approved (Table 8).

For unadjusted weaning weight the Std in Irish Charolais was 3 376. As model 1 had the smallest AIC value of 125 293 this resulted in maximum AIC of: 125 293 + 3 376 = 128 669 and 125 293 + 5 % = 131 558. Independent on calculation method (+ 1 Std or + 5 %) both test model 1 and 2 were approved. The Std in Irish Limousin was 2 330. As model 1 had the smallest AIC value of 71 462 this resulted in maximum AIC of: 71 462 + 2 330 = 73 792 and 71 462 + 5 % = 75 035. Independent on calculation method (+ 1 Std or + 5 %) both test model 1 and 2 were approved (Table 9).

Table 7. British test models for adjusted weaning weight, significance of environmental effects and values of AIC, AICC, BIC and -2 res log likelihood for each test model as well as maximum AIC calculated as + 1 Std and + 5% from the test model with the smallest AIC value

| Breed | No. of observations | | | | | | | | | | |
	Original data	Analyzed data	Model	Significance of fixed effects	AIC	AICC	BIC	-2 res log likelihood	AIC + 1 Std	AIC + 5 %	Approved / Not app.
Limousin	99 262	30 000[d]	1[a]	***	262 449	262 449	262 447	262 447			Not app.
		30 000	2[b]	***	263 114	263 114	263 112	263 112			Not app.
		30 000	3[c]	***	201 623	201 623	201 621	201 621	236 934	211 704	App.

[a] Adjusted national model as described in Material and Methods.
[b] The effect of age of dam (quadratic) was excluded.
[c] An interaction HY*birth month was included.
[d] The number of animals had to be reduced as the memory space was limited.
*** Fixed effects were significant (p < 0.001).

Table 8. Irish test models for adjusted weaning weight, significance of environmental effects and values of AIC, AICC, BIC and -2 res log likelihood for each test model as well as maximum AIC calculated as + 1 Std and + 5% from the test model with the smallest AIC value

| Breed | No. of observations | | | | | | | | | | |
	Original data	Analyzed data	Model	Significance of fixed effects	AIC	AICC	BIC	-2 res log likelihood	AIC + 1 Std	AIC + 5 %	Approved / Not app.
Charolais	14 054	14 054	1[a]	***	124 101	124 101	124 097	124 097			Not approved
		14 054	2[b]	***	112 041	112 041	112 037	112 037	120 569	117 643	Approved
Limousin	8 777	8 777	1[a]	***	70 910	70 910	70 908	70 908			Not approved
		8 777	2[b]	***	61 660	61 660	61 656	61 656	68 201	64 743	Approved

[a] Adjusted national model as described in Material and Methods.
[b] An interaction HYS*sex was included.
*** Fixed effects were significant (p < 0.001).

Table 9. Irish test models for unadjusted weaning weight, significance of environmental effects and values of AIC, AICC, BIC and -2 res log likelihood for each test model as well as maximum AIC calculated as + 1 Std and + 5% from the test model with the smallest AIC value

Breed	No. of observations		Model	Significance of fixed effects	AIC	AICC	BIC	-2 res log likelihood	AIC + 1 Std	AIC + 5 %	Approved / Not app.
	Original data	Analyzed data									
Charolais	14 054	14 054	1[a]	Only HYS and average age were significant (***)	125 293	125 293	125 289	125 289	128 669	131 558	App.
		14 054	2[b]	HYS and sex were significant at *** level, sex*age at weighing at ** level	127 513	127 513	127 509	127 509			App.
		14 054	3[c]	***	131 925	131 925	131 923	131 923			Not app.
Limousin	8 777	8 777	1[a]	Only HYS and average age were significant (***)	71 462	71 462	71 460	71 460	73 792	75 035	App.
		8 777	2[b]	Only HYS (***) and sex (*) were significant	73 347	73 347	73 343	73 343			App.
		8 777	3[c]	***	76 096	76 096	76 094	76 094			Not app.

[a] Adjusted national model as described in Material and Methods.
[b] The effect of average age was excluded.
[c] The effect of average age and the interaction sex*age at weighing were excluded.

*** Fixed effects were significant (p < 0.001).
** Fixed effects were significant (p < 0.01).
* Fixed effects were significant (p < 0.05).

Discussion

National and International genetic evaluations of beef cattle

The structure of the farms rearing beef cattle in the countries included in this study, Sweden, Denmark, UK and Ireland, show many similarities. In general the number of heads per farm is relatively small (Fogh, 2007; Statistics Denmark, 2009; Swedish dairy Association, 2009). However, the total number of cattle reared for beef in the mentioned countries show greater differences. In Sweden the total number of suckler cows reaches twice the size of the Danish suckler cow population. In both countries the average number of cattle is counted in hundred of thousands (Statistics Denmark, 2009; Swedish Board of Agriculture, 2009b). In UK and Ireland this figure is closer to 1.5 million (DEFRA, 2008; Department of Agriculture, Fisheries and Food, 2008). France differs somewhat from the other countries included in this study as not only the total number of cattle reared for beef is much greater but also the number of heads per farm. The total number of beef cattle even exceeds the total number of dairy cattle within the country (Laloë *et al.*, 2007; Ministère de l'Alimentation, de l'Agriculture et de la pêche, 2009).

Independent of population size all countries included in this study have well developed breeding organizations. Information from trait recordings on-farm, at performance test stations or from abattoirs etc. is collected and stored at central databases. This information is extracted from the databases and used for national genetic evaluations. A central organization is responsible for the national genetic evaluations, for example the Swedish Dairy Association in Sweden or the ICBF in Ireland. These organizations set up overall breeding objectives for the different national beef breeds in addition to the more specific breeding objectives set up by each breed society.

The breeding or selection objectives set up by the Charolais and Limousin breeding associations show great similarities both between the breeds and across countries. These mainly include high production at low cost i.e. good growth and high food conversion as well as good carcass classification and high fertility. However, emphasis is also put on health traits, for example good feet and legs, and good mothering abilities such as high milk production (Danish Charolais, 2009; La Limousine, 2009; Swedish Charolais Association, 2009). There do exist some breed specific differences. In Swedish Charolais an especially important breeding objective has been to improve the direct growth rate while maintaining a constant birth weight in order to minimize dystocia and other problems around calving. Though it appears as this objective has been reached successfully (Eriksson *et al.*, 2007) it is still an important part of the breeding programme to avoid undoing all the work. In Swedish, Danish and especially Irish Limousin traits such as temperament and growth rate have received a lot of attention as these have been perceived as weak areas in this breed. The aim is to increase the growth rate without increasing the calving difficulties, something that has already been achieved in Swedish Charolais. Selection for more docile animals appears to have been successful in Ireland (Irish Limousin Cattle Society, 2009).

In Sweden rearing specialized beef breeds is a relatively new phenomenon and apart from keeping small herds many farmers also work part time outside the farm. The genetic evaluation of beef cattle using BLUP procedures has only been in place since 2000. The traits

evaluated include birth weight, daily gain from birth to 200 days, daily gain from 200 days to 365 days, carcass fatness, fleshiness and net gain from birth to slaughter as well as calving ability at first calving. Carcass and calving traits were added to the evaluation as late as 2005. The Swedish evaluation is still heavily based upon records from purebred animals and no cross breeding effects are included in the evaluation as for example in the Irish genetic evaluation (Taurus, 2005; Eriksson *et al.*, 2007; Evans *et al.*, 2007). The situation is similar in Denmark, yet they still have implemented a more complex genetic evaluation. The Danish genetic evaluation includes a greater number of traits compared to the Swedish and include both purebred and crossbred individuals. The purpose of including a large amount of information is to achieve high reliabilities of the EBVs (Fogh, 2007) and may benefit each individual Danish beef breed society. The French genetic evaluation of beef cattle have been in operation since 1991 and includes the traits calving ease, birth weight, 120- and 210-day weights, linear scores, carcass weights, EUROPA muscular scores and slaughter age. As the younger Swedish evaluation it only includes purebred animals (Laloë *et al.*, 2007).

In UK and especially in Ireland the breeding objectives include many different traits. These traits are related to both production and health. By including a large number of traits the breeding work in each breed society is facilitated as it is possible to select animals on merits that are in accordance with the selection objectives set up by the breed societies (Coffey *et al.*, 2007; Evans *et al.*, 2007). The drawback of including a large number of traits is that it is time consuming to perform all measurements and may become expensive.

So far the results of the international genetic evaluation performed by Interbeef are not official but they are shared with the participating countries. The only trait included in the evaluation is adjusted weaning weight (Venot *et al.*, 2007). This is an economically important trait and it has been suggested that recording of weaning weight is the first step to a successful breeding program (Sellers *et al.*, 1970). Similar to the countries included in this study the model used by Interbeef is a multiple trait animal model (Phocas *et al.*, 2005; Coffey *et al.*, 2007; Eriksson *et al.*, 2007; Evans *et al.*, 2007; Fogh, 2007; Venot *et al.*, 2007; Interbeef, 2009). Though Interbeef only evaluate weaning weight in purebred animals so far, more traits are likely to be added to the international genetic evaluation in the future. Possible new traits considered important by the member countries of Interbull include carcass weight and conformation as well as calving difficulty (Forabosco *et al.*, 2009a). As cross breeding is a very common occurrence in beef production, it is also likely that crossbred animals will have to be included eventually and cross breeding effects such as heterosis and recombination will have to be considered in the model. Inclusion of genomic information in the international genetic evaluation of beef cattle is being investigated and in some cases implemented at a national level but still appears to lie in the future at an international level. So far genomic selection mainly concerns dairy cattle.

A joint genetic evaluation between Canada, the US and Uruguay was found to be feasible in studies by de Mattos *et al.* (2000) and Lee & Bertrand (2002). The trait investigated was adjusted weaning weight the same as in Interbeef, however, the breed of cattle differed. In Interbeef the genetic evaluation is performed using records from purebred Charolais and Limousin as these are among the largest breeds in the participating countries. The breed investigated by de Mattos *et al.* (2000) and Lee & Bertrand (2002) was Hereford.

As the countries participating in Interbeef are limited the Europe, so far, it is possible that any genotype × country interactions that may occur are relatively weak similar to the situation observed by de Mattos *et al.* (2000) between Canada, the US and Uruguay. However, as more

countries join Interbeef these interactions will play a more important role and it may be necessary to take a similar approach as in Interbull where genotype × country interactions are considered in the MACE procedure (Interbull, 2009a).

Validation method A

In the Danish dataset on adjusted weaning weight the effect of sex had zero degrees of freedom and as a consequence the significance was not calculated. In the case of Ireland when unadjusted weaning weight was analyzed, the effects sex and average age at weighing were included as main effects as well as in an interaction between the two (see test model 1). As a result only HYS and average age were found to be significant in model 1 for both breeds. Instead of including both sex and age at weighing as main effects as well as an interaction it would have been sufficient to include only the interaction in test model 1 (Table 9).

In most cases the fixed effects included in the different test models were significant. This has the implication that in all generated test models where an effect was excluded the information criterions and likelihood values increased. Because even though overparameterization is penalized, the exclusion of significant effects probably caused the models to loose some level of explanation. On the other hand when interactions were included, such as HY*season in the case of Denmark, HY*birth month in the case of UK or HYS*sex in the case of Ireland, the information criterions and likelihood values decreased (Table 4, 5, 6, 7, 8, 9). This may be explained by the fact that very significant main effects are more likely to display strong interactions, which in turn will affect the model fit (Weiss, 2005). By including relevant interactions between main effects of high significance it is possible to increase the level of explanation and achieve a better model fit.

This explains why, in tests on adjusted weaning weight, test model 1 for the Swedish Charolais and Limousin is the only approved model or in the case of UK model 3. The exclusion of the interaction HYS*sex in the Swedish test model 2 and 3 renders much higher AIC values which will lie outside the maximum approved AIC. In case of the British test models the inclusion of the interaction HY*birth month renders test model 3 a much lower AIC compared to model 1 and 2. Test model 1 and 2, therefore, lie outside the maximum approved AIC value (Table 4, 7).

Independent of country, breed and test model the AIC and AICC values were found to be identical. This was also the case for BIC and -2 res log likelihood. These results indicate that the sample sizes are large enough that the AICC converge into AIC. Only small differences was observed between AIC/AICC and BIC/-2 res log likelihood values, with BIC and -2 res log likelihood having the smallest values in all cases (Table 4, 5, 6, 7, 8, 9). This may be a result of differences in the AIC equation IIa and BIC equation III. However, in all cases AIC/AICC and BIC/-2 res log likelihood target the same models. In this study only three relatively similar models were tested and compared. In a situation where more models displaying larger differences are tested it is more likely that the target models may differ between the AIC and BIC, but this also depends on sample size, tapering effects, number of effects included in the models and whether the models are nested or not. It appears as though AIC performs better when there exist tapering effects and BIC when only a few big effects are included in the models. Usually information criterions are preferred to the maximum likelihood principle as more parsimonious models are achieved (Burnham & Anderson, 2004). In this study the final ranking and model approval in each country and breed was based on the AIC.

Due to limited memory space it was necessary to decrease the number of animals in the Swedish Charolais, Danish Limousin and British Limousin datasets (table 4, 5, 6, 7). In the case of both Danish Charolais and Limousin animals with the odd sexes 3 and 4 were excluded from the analyses. As the sample size affect the AIC (Burnham & Anderson, 2004), different values might have been obtained if all animals in the datasets could have been included in the study.

Ireland is a special case as a lot of information concerning the fixed effects included in the national model was lacking from the data files submitted to Interbeef. According to the Interbeef form the following fixed effects are included in the Irish national model: HYS, HYS for previous herd, sex, age at weighing and parity of dam. The model also includes the interactions sex*age at weighing, sex*age at weighing*age and sex*age at weighing*age*age. HYS for previous herd, sex*age at weighing*age and sex*age at weighing*age*age are not of interest here as they relate to crossbred animals (Interbeef, 2009). Still, the datafiles only contained information on HYS and sex in the case of the trait adjusted weaning weight. As it is not possible to compare AIC values between datasets it follows that it is not possible to compare countries due to differences in national models, recording methods, sample sizes etc. Therefore, the low AIC values in case of the Irish test models do not indicate that the Irish models have a better fit than the other countries' national models. Such a comparison is only possible within country and breed as well as trait if the models differ between traits.

Test model 1 on unadjusted weaning weight in Danish Charolais resulted in AIC values similar to those in case of adjusted weaning weight. No other comparisons are possible as both test models 2 and 3 in both Danish Charolais and Limousin differ between the two traits and in the case of Limousin the sample sizes differ as well (Table 5, 6).

The Irish test models 1 and 2 for unadjusted weaning weight included more effects compared to the test models for adjusted weaning weight. In Irish Charolais the inclusion of more effects resulted in AIC values which showed a greater similarity to those of the other countries in case of both adjusted and unadjusted weaning weight. The much lower values still obtained in case of Irish Limousin were probably related to the smaller sample sizes (Table 8, 9).

When the trait adjusted weaning weight was analyzed the same results were achieved whether + 1 Std or + 5 % were used to calculate AIC ranges (Table 4, 5, 7, 8). In case of Denmark, when unadjusted weaning weight was analyzed, + 1 Std proved to result in a lower upper limit of the AIC value thereby excluding more tests models compared to + 5 % (Table 6).

Based on these results a possible validation method A is suggested to consist of:

i) Description of three or more test models including results regarding AIC and perhaps BIC as well as log likelihood of these.
ii) Selection of the model with the lowest AIC value or another approved model. The AIC value of an approved model is not allowed to differ more than 5 % from the model with the lowest AIC within the test battery.
iii) Inclusion of pedigree information is optional.
iv) Countries may use a statistical software package of their own choice.
(Forabosco *et al.*, 2009b also see appendix 1)

This is only a first draught for a possible validation method A, which still has a number of limitations. A drawback with this method is that it is time consuming and requires a lot of memory space as the estimation of fixed effects in mixed models is a complex procedure. A strategy to overcome this problem has to be drawn up for countries with large datasets, for example France. Another issue that may arise concerns the kind of test models used by the countries, as this is not possible to control. One problem when designing the test battery of models is that only effects that are included in the data sent to Interbeef can be tested. It is not possible for Interbeef to add and test for any other effect that might be significant and it is probable that the model already in use will prove to be the best model. Therefore it is necessary that the countries, in the files submitted to Interbeef, include all effects that have been tested even those excluded in the final and approved model suggested by the countries.

It may be possible to apply this validation method to both traits, adjusted and unadjusted weaning weight, analyzed here. However, more tests are necessary to say whether this is true in all cases. Compared to the validation methods implemented in the international genetic evaluation of dairy cattle, validation method A does not consider genetic trends. A method B has to be developed and implemented to investigate the quality and stability over time of the genetic trends (Boichard *et al.*, 1995; Forabosco *et al.*, 2009b also see appendix 1). By investigating genetic trends it would also be possible to detect systematic trends and, similar to the assumption in the Interbull method 3, successive evaluations of any individual would be expected to be close to or equal to their true BV and that new information should only result in random variation. Again method B would have to be especially adapted to beef data as the Interbull method 3 is based on official predicted genetic merit whereas Interbeef only receive raw data. This would also give support to validation method A, because it would make it possible to elaborate more on the actual quality of the national genetic evaluation models. It is difficult to say whether a model is of good quality or not solely based on its AIC value as it is not clear what value is to be expected of a model with good fit. Investigation of genetic trend would be possible as the datafiles submitted to Interbeef from the participating countries contain observations that date relatively far back, in the case of UK for example the first records are from 1972.

Conclusion

The organization of the breeding work, such as trait recording and access to large databases, is well developed in all countries included in this study. Therefore, submitting data of high quality should not present an issue. Still, there exist problems in this area especially in the case of Ireland where a lot of information on the effects included in national model is lacking in the data files submitted to Interbeef. This present a problem as this will affect estimates of IBVs in a negative way for Irish animals.

The models used in each individual country appear to be of good quality. In some cases inclusion of additional relevant interactions may need to be considered, for example is the combined effect of herd, year and season to prefer to the effect of only herd and year.

The validation methods used by Interbull in the international genetic evaluation of dairy cattle are based on data that show very few similarities with the data submitted to Interbeef. Here a validation method A is suggested which is adapted to data from beef cattle. This method is based on the AIC of three test models. Models approved for selection are either the model with the lowest AIC or models that do not differ more than + 5 % from the model with the lowest AIC. To participate in the international genetic evaluation performed by Interbeef countries have to implement validation method A at first entry and when national models are

modified. All effects that have been tested by the country have to be included in the files submitted to Interbeef.

Inclusion of genomic information in the national genetic evaluations of dairy cattle is becoming more common and may soon be included in the international evaluation. Both at a national and international level the genetic evaluation of beef cattle is lagging behind in this area. Some countries (i.e. France and UK) have recently started to collect genomic information for beef cattle. In the future, SNP information should be integrated with phenotypic information but more imminent work relates for example to expansion of the evaluation to include more traits, such as carcass and calving traits, and effects related to crossbreeding as well as investigation of genetic trends.

Acknowledgements

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Appendix 1

Validation method for beef national genetic evaluation models

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Abstract
Interbeef receives data, pedigree and statistical models for Charolais and Limousin breeds from member countries. The quality of data and pedigree information is checked before they are used for an international genetic evaluation. This paper presents an attempt to validate the quality of national statistical models for beef cattle. The method aims to evaluate the soundness of national models using advanced statistical tools; the Akaike information criterion (AIC), the Bayesian information criterion (BIC) and the –2 log likelihood (Log L). AIC, BIC and Log L give similar results and in the majority of cases countries provided good statistical models. This method is easy to integrate into the national genetic evaluation system, it's flexible but the memory space required can be a limiting factor.
Keywords: information criterion, national models, beef cattle, Interbeef

1. Introduction

Currently at Interbull the genetic trends for dairy national data are validated using the three methods first developed by Boichard *et al.* (1995) and based on the function of observed vs. expected genetic trends. Weller *et al.* (2003) implemented Interbull validation Method 3 based on the empirical confidence interval for the number of new daughters per bull (δ) computed using the nonparametric bootstrap. Lidauer *et al.* (2005) made Interbull validation Method 2 more robust by using the daughter deviations of a sire by the birth year of the daughters. Unfortunately, validation Methods 1, 2 and 3 (Interbull, 2009) cannot be used to validate national beef models because:

1) Interbeef receives raw data from the member countries (i.e. for the time being only adjusted and unadjusted weaning weights) while Interbull receives proofs for dairy traits (i.e. BV or TA for production, udder health, conformation, etc.). Method 1 for dairy uses breeding values (BV) or transmitting abilities (TA) while beef data do not include this information. For this reason Method 1 (Interbull, 2009) cannot be used as validation method for beef data or statistical models.
2) Method 2 (Interbull, 2009) is based on the DYD information, which investigates the non-genetic time trend over the entire period considered in the national evaluation. Interbeef receives raw data for males and females and because the trait is measured on the animal itself, daughter yield deviation (DYD) is not provided and therefore the method is not suitable for beef data.
3) Method 3 (Interbull, 2009) analyzes the official national predicted genetic merit variation across evaluation runs for dairy data and it is designed specifically for bulls' predicted genetic merit which is not included in the beef data. Therefore, Method 3 cannot be used to validate beef data or statistical models.

Jorjani (2003) pointed out the importance of having a validation method in place which includes a validation not only for dairy data but also for national dairy models. Interbull has not yet developed a validation method for national models for dairy cattle although validation of expected genetic trends can be considered as an indirect measure of the goodness of the national model applied.

A method to validate national statistical models should be:
  1) Able to detect potential errors
  2) Easy to use for the member countries
  3) Flexible

The aim of this paper is to present:
  a) A method to validate national statistical models for beef cattle.
  b) The limits of the method.

2. Material and Methods

Data and pedigree information

Countries provided data and pedigree information for each breed and trait combination following the Interbeef guidelines (Interbeef, 2009b) for the Interbeef project (Venot et al., 2007; Forabosco et al., 2008). Five countries (Table 1) have provided data, pedigrees and models for Charolais and Limousin breeds for adjusted weaning weight. Interbull has received a total of 3,118,878 performance and 3,742,857 pedigree data for the Charolais breed, and 1,973,112 performance and 2,582,960 pedigree data for the Limousin breed.

Data and pedigrees were transferred via ftp server. Data quality was checked and programs have been developed to detect potential errors.

Models

The quality of national statistical models provided by member countries must be checked before they can be used in an international genetic evaluation. Setting up a good national model is an essential key for a reliable international genetic evaluation (Jorjani, 2003). Models are provided by member countries using the Form Beef (Interbeef, 2009a). A short summary of national models for adjusted and unadjusted weaning weight are provided in Table 2.

Information criterion (IC)

There are a number of methods available to investigate the fit of the model to the data using a variety of statistical tools that may be implemented, depending on the statistician's school of thought, for example R^2, RMSE, deviance, or formal χ^2 goodness-of-fit, etc.

In any case, modern statisticians, prefer to use the "information criterion=IC" for a more parsimonious model (principle of parsimony being defined by Box & Jenkins, 1976 as a model with the smallest possible number of parameters for adequate representation of the data).

The Akaike information criterion (AIC) is a measure of the goodness of fit of an estimated statistical model. The AIC is not a test of the model in the sense of hypothesis testing; rather it is a tool for model selection (Burnham and Anderson, 1998). Given a data set, several competing models may be ranked according to their AIC, with the one having the lowest AIC being the best. From the AIC value one may infer that, for example, the top models are in a tie (less then 5% difference between top models) and the rest are far worse (Burnham and Anderson, 1998).

In the general case, the AIC is defined as:

$$AIC = 2k - 2\ln(L)$$

Where k is the number of parameters in the statistical model and L is the maximized value of the likelihood function for the estimated model.

AIC value assigned to a model is only meant to rank competing models and tell you which is the best among the given alternatives. The absolute values of the AIC for different models have no meaning; only relative differences can be ascribed meaning.

The Bayesian information criterion (BIC), is a criterion for model selection among a class of parametric models with different numbers of parameters. BIC is very closely related to the AIC. In the general case, the BIC is defined as:

$$BIC = -2\ln(L) + k\ln(N)$$

Where N is the number of datapoints used to fit the model and k is the number of parameters to be estimated. Given any two estimated models, the model with the lower value of BIC is the one to be preferred. BIC can be used to compare estimated models only when the numerical values of the dependent variable are identical for all estimates being compared.

The -2 log likelihood (Log L) is a probability density function (PDF) which is used to examine the trade off between goodness of fit and parsimony.

3. Results and Discussion

A statistical package (SAS, 2009) was used to calculate AIC, BIC and Log L (Tables 3 and 4). Mixed model procedures (PROC MIXED) were utilized to compute statistical analysis. For each trait and country-breed combination, three tests were conducted and the statistical models were ranked giving the best ranking to the lowest IC value. In all cases the difference between AIC, BIC and Log L were very small

and values were almost identical. An example is given in Table 3 and 4.

In Tables 3 and 4 the models proposed by the member countries were always the best among all models tested. Model 2 and model 3 were generated by the authors to evaluate the goodness of fit of the original model. Both models were obtained changing the effects of the original model but no further assumptions were made when the models' structures were generated.

In some cases (i.e., Limousin data from the UK, Table 3) the difference between model 1 and model 2 was very small (less than 5%). When the difference is reasonably small (less than 5%), both models can be considered "the best model" and countries can choose between them.

In other cases, (i.e. Limousin and Charolais data from Denmark, Table 4) all 3 models analyzed were approved because the difference between AICs was less than 5%.

3.1 Limits of this method.

- Estimating all fixed effects is time consuming and in case of complex models the memory space required is a limiting factor.
- This validation method does not include the quality and the stability of the genetic trends over time. A robust validation method needs to include the analysis of genetic trends. For this reason Method A that would fit beef data, national models and genetic trends needs to be developed.

4. Conclusions

Results for all country-breed combinations for AIC, BIC and Log L were analyzed. In the majority of cases the models provided by countries (national models) were the best models with the lowest information criterion. In some cases the model provided by member countries (national model) was among the best models (with an information criterion that differed no more than 5% from the model with the lowest one).

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Table 1. Number of animals in the pedigree and performance files.

	Pedigree			Performance	
Country	Charolais	Limousin		Charolais	Limousin
France	3,474,958	1,968,574		2,999,172	1,813,211
Ireland	39,337	23,878		14,115	8,826
UK	-----	129,068		------	99,262
Denmark	125,548	270,180		14,067	35,289
Sweden	103,014	191,260		91,524	16,524
Total	3,742,857	2,582,960		3,118,878	1,973,112

Table 2. National models provided by countries[1] for adjusted and unadjusted weaning weight (w.w.).

	Adjusted w.w.			Unadjusted w.w.	
Country	Charolais	Limousin	Country	Charolais	Limousin
Sweden	HYS*Sex,Sea, Aged, Mbirth	HYS*Sex,Sea, Aged,Mbirth	Denmark	HY,Sea,Aged*Par,Sex,, Tw,Agewei	HY,Sea,Aged*Par,Sex,, Tw,Agewei
UK	----	HY, Bmonth, Sex, Btype,Aged(lin.,qua.)	Ireland	HYS,Sex,AAgewei,Sex * AAgewei(cov), Sex* AAgewei^2(cov), Sex* AAgewei^3(cov)	HYS,Sex,AAgewei, Sex* AAgewei(cov), Sex* AAgewei^2(cov), Sex* AAgewei^3(cov)

Note:HYS=Herd*Year*Season, Sea=Season of calving, Aged=Age of the dam, Agew=Age at weaning, Agewei=Age at weighing, AAgewei=Average age at weighing, Bmonth=Birth month, Btype=Birth type, Mbirth=multiple birth, Par= parity, Tw=Twin, lin=linear, qua=quadratic, cov=covariante.[1] For the full list of countries and models visit: http://www-interbull.slu.se/Interbeef/genev/framesida-genev.htm

Table 3. AIC, BIC and Log L for adjusted weaning weight for Charolais and Limousin breeds

Cou [1]	Breed [2]	Model	Description of model	AIC	BIC	LogL	Rank	App./ Not app.
Swe	Cha[5]	1	National model[3]	615406	615402	615402	1	App
Swe	Cha[5]	2	No interaction between HYS and Sex	647303	647301	647301	2	Not App.
Swe	Cha[5]	3	No interaction between HYS, Sex, no Sea	655440	655438	655438	3	Not App.
Swe	Lim	1	National model(3)	132184	132182	132182	1	App
Swe	Lim	2	No interaction between HYS and Sex	141326	141324	141324	2	Not App.
Swe	Lim	3	No interaction between HYS, Sex, no Sea	141381	141379	141379	3	Not App.
UK	Lim[6]	1	National model(3)	98039	98035	98035	1	App.
UK	Lim[6]	2	Interaction HY* Bmonth, no Aged(lin.,qua)	99754	99750	99750	2	App.
UK	Lim[6]	3	No effect of Aged (lin.,qua.)	130796	130792	130792	3	Not App.

[1] Cou=country, Swe=Sweden, UK=United Kingdom; [2] Cha=Charolais, Lim=Limousin; [3] For model description see Table 2. [4] Approved /not approved=Models are approved when they are ranked 1st or alternatively the AIC value differs no more than 5% from the model with the lowest AIC value. [5] A random sample of 70.000 animals. [6] A random sample of 15.000 animals

Table 4. AIC, BIC and Log L for unadjusted weaning weight for Charolais and Limousin breeds

Cou [1]	Breed [2]	Model	Description of model	AIC	BIC	LogL	Rank	App./ Not app.
Dnk	Cha	1	National model(3)	115089.0	115085.0	115085.0	1	App
Dnk	Cha	2	No Aged*Par and no Tw	116294.6	116290.6	116290.6	2	App
Dnk	Cha	3	No Aged*Par, no Tw, no Sea	116543.6	116539.6	116539.6	3	App
Dnk	Lim	1	National model(3)	286406.0	286402.0	286402.0	1	App
Dnk	Lim	2	No Aged*Par and no Tw	288374.8	288370.8	288370.8	2	App
Dnk	Lim	3	No Aged*Par, no Tw, no Sea	289104.8	289100.8	289100.8	3	App
Irl	Cha	1	National model(3)	125293.1	125289.1	125289.1	1	App
Irl	Cha	2	No Agewei	127512.5	127508.5	127508.5	2	App
Irl	Cha	3	No Agewei, no all cov	131925.0	131923.0	131923.0	3	Not App
Irl	Lim	1	National model(3)	71461.8	71459.8	71459.8	1	App
Irl	Lim	2	No Agewei	73346.5	73342.5	73342.5	2	App
Irl	Lim	3	No Agewei, no all cov	76095.8	76093.8	76093.8	3	Not App

[1] Cou=country, Dnk=Denmark, Irl=Ireland; [2] Cha=Charolais, Lim=Limousin; [3] For model description see Table 2. [4] Approved /not approved=Models are approved when they are ranked 1st or alternatively the AIC value differs no more than 5% from the model with the lowest AIC value