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**GENETIC EVALUATION STRATEGIES
FOR MULTIPLE TRAITS AND COUNTRIES**

A Thesis

Presented to

The Faculty of Graduate Studies

of

The University of Guelph

by

PETER G. SULLIVAN

In partial fulfilment of requirements

for the degree of

Doctor of Philosophy

May, 2002

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ABSTRACT

GENETIC EVALUATION STRATEGIES FOR MULTIPLE TRAITS AND COUNTRIES

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Genetic evaluation strategies for multiple traits in multiple countries were studied using simulated data for three lactation traits in each of two importing and two exporting countries. Pedigree-selected young males were progeny-tested within each country. Proven males with higher predicted genetic merits were mated to higher proportions of the female population, and the very best proven males were used internationally. Females were culled at a rate of 33%, based on phenotypic performance in the most recent lactation. Conversion (CNV), multiple-trait across-country evaluation (MACE) and global animal model (GAM) strategies were considered. Base populations were either unselected, or selected with three alternative levels of semen exchange among countries. Selection in base populations included truncation selection of males in all countries, and higher genetic means for the exporting relative to importing countries. With unselected base populations, errors of prediction (ERP) for top (highest predicted genetic merit) bulls were equivalent ($P>.10$) for MACE and GAM strategies. The GAM had lower ERP than MACE strategies ($P<.01$) for all bulls, but MACE strategies reduced ERP relative to CNV by 88% of the corresponding reduction for GAM. With selected base populations, MACE strategies had lower ERP than GAM for top and all bulls ($P<.01$) if semen exchange was low, and equivalent ERP if semen exchange was high ($P>.10$). The ERP for MACE and CNV strategies were consistently smaller if the strategies allowed multiple, rather than one trait per country. Comparisons of

country populations were biased for all strategies with both unselected and selected base populations, due to missing data and implied assumptions about genetic group effects. The biases were largest, and directly responsible for higher ERP, with the GAM strategy if base populations were selected. Modifications to account for selection in MACE eliminated biases ($P > .10$) if base populations were unselected, and reduced biases by approximately one half if base populations were selected. MACE strategies modified to account for selection always had the lowest ERP among all strategies for all bulls. The modifications to account for selection in MACE are also recommended for national evaluation systems to reduce biases in sub-population comparisons when pedigree data are incomplete.

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Glossary of Terms

BV: true breeding value of an animal.

CNV: linear conversion.

country bias: bias in the comparison of genetic means of animals from different countries.

country scale: genetic evaluation scale of a country.

EBV: estimated breeding value of an animal.

ERP: square root of the mean squared error of prediction.

GAM: global animal model.

lactation trait: a trait expressed for a given lactation (e.g. first lactation milk yield or third lactation protein yield).

MACE: multiple-trait across-country evaluation.

MME: mixed model equations.

NAM: national animal model.

pedigree-selected: selected based on pedigree information.

progeny-tested: evaluated and selected based on progeny performance information.

selection-modified MME: mixed model equations that have been modified to account for selection effects in the data being analyzed.

selection-modified MACE: a MACE strategy based on selection-modified MME.

selection-modified GAM: a GAM strategy based on selection-modified MME.

1. INTRODUCTION

Genetic evaluation of livestock with the use of advanced statistical techniques has become widespread around the world. The number of countries that compute genetic evaluations, and the sophistication of within-country genetic evaluation strategies, have increased dramatically over the last 20 years. Genetic improvement systems have also grown in their level of sophistication, and now commonly include global sourcing of breeding stock, usually in the form of semen or embryos.

International genetic evaluation strategies, which are required to compare individuals from multiple countries, are also evolving. With dairy cattle populations, for example, linear conversion equations were used to predict genetic merits of sires in foreign countries, based originally on ordinary least squares and subsequently with alternative methods proposed by Goddard (1985) and Wilmink et al. (1986). The conversion equation strategies were eventually replaced by a strategy called Multiple-trait Across Country Evaluation (MACE), developed by Schaeffer and Zhang (1993). The evolution of strategies for international evaluation of dairy cattle has been heavily influenced by an organization called Interbull, which will be discussed in section 2.2.

The MACE strategy, first applied to dairy production traits in 1994 (Interbull, 1999), allowed only one trait per country, but could be repeated in separate analyses for each trait of interest. The MACE strategy has been refined many times by Interbull, based on research findings by Sigurdsson et al. (1996), Schaeffer et al. (1996), Rozzi and Schaeffer (1996), Weigel and Banos (1997), Sullivan (1999) and Fikse and Banos (2001). Dairy conformation traits (Klei and Lawlor, 1998; 2000) and health traits (Mark et al.,

2000) are now routinely evaluated by Interbull using MACE strategies that are similar to the MACE strategy used for production traits.

Each of the MACE strategies currently used by Interbull are limited to simultaneous analysis of a single trait per country, and could be improved further by refining MACE to accommodate multiple traits per country. Schaeffer (2001) proposed modifications to MACE that would accommodate multiple traits per country, but additional modifications are still required to account for differences in national data structures and genetic evaluation strategies, as was done recently for MACE with one trait per country (Fikse and Banos, 2001).

Lohuis and Dekkers (1998) and Weigel and Rekaya (2000) proposed global animal model (GAM) strategies that could replace MACE. The GAM has some theoretical advantages over MACE, but is more difficult computationally, and even at the national level may only be feasible with simplified models (Wiggans and Goddard, 1996; Jamrozik et al., 1997). The GAM may not be computationally feasible for international evaluations of Holstein cattle for multiple traits in multiple countries. Violation of model assumptions may also affect the relative advantages of GAM, particularly the often violated assumption that data available for genetic evaluation are unaffected by selection (Schaeffer et al., 1998).

Recently proposed strategies for international genetic evaluation of beef cattle have included multiple traits per country with a GAM, but for a limited number of countries and with simplifications that ignore differences in genetic expression of traits in each country (deMattos et al., 2000a, 2000b; Lee and Bertrand, 2002).

The objectives of this thesis were to compare conversion, MACE and GAM strategies for evaluation of multiple traits in multiple countries, with or without violated assumptions about selected data. Monte Carlo simulations were used and strategies were compared in terms of genetic prediction error, bias of country comparisons, efficiency in predicting genetic superiority, and ease of application.

2. LITERATURE REVIEW

2.1. The Mixed Model Equations

Genetic improvement is achieved by selecting and mating individuals that are better than average for one or more desirable characteristics or traits. Selection in livestock populations is often for quantitative traits, which exhibit continuous variation and can be measured on a continuous scale. Quantitative traits are generally influenced by many genes (Falconer, 1981). The genetic value of an individual for a particular quantitative trait is the sum of independent individual gene effects plus any gene interaction effects. The distribution of genetic values in a population is therefore a distribution of a sum of random variables, which by the central limit theorem (Mood and Graybill, 1963) approaches normality for a large number of contributing genes. This leads to what is commonly referred to as the infinitesimal genetic model (Kennedy, 1993) that is assumed for most genetic evaluation systems in use today for livestock.

The assumption of normality for the distribution of genetic values has enabled the use of very powerful techniques to predict genetic values of individuals from phenotypic performance data measured on farms. In particular, the mixed model equations (MME) of Henderson (1984), which were developed in the early 1950s under the assumption of normally distributed genetic values, have been used repeatedly for genetic evaluation of livestock.

The MME require specification of first and second moments of all random effects in the model. In a statistical framework, when first and second moments of random effect distributions are known, the MME yield Best Linear Unbiased Estimates (BLUE) of fixed

effects and Best Linear Unbiased Predictions (BLUP) of random effects (Henderson, 1984). While the distribution parameters of random effects are usually not known with certainty, the means can be defined as null and the variances estimated from the available data (Sorensen and Kennedy, 1986).

Henderson's discovery of the MME was motivated by the problem of ranking animals genetically based on badly balanced data that were influenced by a combination of genetic and environmental factors (Searle, 1991; Schaeffer, 1991). Least-squares techniques available at the time did not account for covariances among the genetic effects of related individuals, and selection index procedures (Van Vleck, 1993) did not allow for simultaneous estimation of genetic and environmental effects.

Henderson's MME have been recommended for use in teaching statistics, because of the flexibility of the MME for fitting a variety of fixed plus random effects models, and the simplicity of accounting for correlations among random effects (McLean et al., 1991). This flexibility of the MME has facilitated a continuous evolution of genetic evaluation systems applied to livestock improvement.

Early applications of the MME were limited to research herds or small populations for two reasons. Firstly, computer power was limited both in terms of speed and available working memory. Secondly, the MME for genetic evaluation includes an animal genetic relationship matrix of order equal to the number of animals evaluated. The animal relationship matrix had not only to be formed but also inverted. Therefore, substantial memory and computing time were required to build the MME for genetic evaluation of livestock populations of any appreciable size.

The latter problem was eliminated, for models containing only the additive portion of each animal's genetic effect, when Henderson (1975a, 1975c, 1976) discovered an efficient procedure to create the inverse of the animal relationship matrix directly, and applications of the MME to animal breeding situations quickly followed. The earlier applications for national evaluations were for genetic evaluation of sires of performance recorded animals for a single trait of interest (Schaeffer and Wilton, 1975; Wilton et al., 1975). Multivariate MME were also feasible and were applied primarily for combinations of growth traits in meat species of livestock for sires of recorded animals across herds (Schaeffer and Wilton, 1981). "Sire models" were used because, with several progeny per sire, the MME were much smaller and more manageable if limited to sires only.

Smaller MME could also be built by evaluating a single herd at a time (Pollak and Quaas, 1981) but within-herd evaluations were not useful for selection across herds. Methods were also proposed by Henderson (1975b) to incorporate prior sire evaluations from across-herd MME into a new set of MME to evaluate all animals in a single herd. Van Vleck (1982) and Schaeffer (1983) studied these methods in detail. Comparable procedures were also proposed by Wilson et al. (1985) and Wiggans and VanRaden (1990).

As computer speed and memory increased, MME involving all recorded animals and their ancestors from all herds could be solved and "animal model" genetic evaluation applications began to surface. Single-trait animal models were more common but there were also multiple-trait applications (Benyshek et al., 1988). The multiple-trait methods were useful to reduce genetic prediction error variances (Schaeffer, 1984) and selection

biases (Pollak et al., 1984), and enabled genetic effects to be partitioned between direct contributions of the animals and maternal contributions of dams (Trus and Wilton, 1988; Dekkers, 1994).

Multiple-trait methods are also useful to combine information from multiple indicator traits of the same objective. For example, mastitis resistance is an objective trait of interest in dairy cattle breeding but is more difficult to measure and evaluate directly than an indicator trait such as somatic cell counts. Mastitis resistance and somatic cell counts can be evaluated jointly to increase rates of genetic improvement for the objective trait (Gengler and Groen, 1997). Survival traits are another example, and MACE strategies have been used to combine information on multiple traits related to survival (Jairath et al., 1998; Druet et al., 1999).

Algorithms have been developed to solve large MME for genetic evaluation of livestock (Schaeffer and Kennedy, 1986; Misztal and Gianola, 1987; Misztal et al., 1987), and to simplify computations for multiple trait evaluations (Ducrocq and Besbes, 1993).

Despite these advances, genetic evaluation systems were generally limited to within-country or within-region populations until 1994, when the first international genetic evaluation service for dairy sires was introduced using a multiple-trait sire model (Interbull, 1999).

2.2. International Genetic Evaluations

The limitations of applying the MME to small numbers of animals prevented their use for large-scale genetic evaluation of international populations. International genetic comparisons were needed, however, to facilitate efficient trade of cattle genetics among

interested countries. In 1983, the International Bull Evaluation Service (Interbull) was established to improve international comparisons of cattle. Interbull coordinated research efforts in the area of international genetic evaluations, developed standards and recommended procedures for comparing sires from multiple countries (Interbull, 1990). Interbull also recommended that for national evaluations, sire models be replaced by animal models, or at least by sire-maternal-grandsire (SMGS) models where feasible. Animal model systems are now used to evaluate dairy production traits by almost all of the Interbull member countries (Jorjani, 2000).

In 1994, Interbull implemented its first international genetic evaluation service for dairy sires (Interbull, 1999) using a SMGS international model to combine national EBV from each country participating in the service. The Interbull approach used an MME-based system called Multiple-trait Across-Country Evaluation (MACE), proposed originally by Schaeffer and Zhang (1993), formalized by Schaeffer (1994) and refined by Schaeffer et al. (1996). The evolution of methods leading up to MACE included a number of regression and MME-type approaches, as described in detail by Klei (1995) and Mark (1999). The MACE model is described as a SMGS model, but input EBV from each country are typically computed from animal model systems. A deregression procedure is used to account for covariances among the input EBV of genetically related sires (Sigurdsson and Banos, 1995b; Rozzi and Schaeffer, 1996; Jairath et al., 1998).

The genetic expression of a trait is allowed to vary among countries with MACE, allowing for differences in trait definition, data recording, national evaluation models, etc. The result is that for every trait evaluated through MACE, there is a separate EBV for each sire in every country. The order of the MME for MACE is approximately equal to the

number of animals (sires plus male ancestors) from all countries times the number of countries.

The MACE approach has provided flexibility for international evaluation because it allows for any national genetic evaluation system in participating countries. This flexibility facilitated rapid expansion of the Interbull service, with the number of participating countries increasing from less than 10 to more than 20 between 1994 and 1997 (Interbull, 1999). The increase in number of participating countries slowed after 1997 and there were 25 participating countries by 2001. The service, which originally included production traits only, was expanded to include additional traits and now includes routine MACE evaluations for three dairy production traits, 18 conformation traits and two udder health traits (Interbull, 2001b).

Each trait is evaluated separately by Interbull, because the MACE model allows only one trait per country. Schaeffer (2001) extended the theory of MACE to allow for multiple traits per country in a simultaneous analysis, but the extended model has not yet been implemented in practice. The extended model should be feasible computationally for a large number of traits per country, as long as all required covariances can be estimated reliably. Covariance component estimation for MACE will be discussed in section 2.5.

Concerns about data quality have been discussed repeatedly because of the number of countries that are allowed and encouraged to participate in MACE. Methods to validate genetic trends in national EBV have been developed (Bonaiti et al., 1994; Boichard et al., 1995) as one way of ensuring quality in the national EBV used for MACE, and Interbull monitors changes in sequentially submitted national EBV from each country. Additionally,

Interbull has proposed that trends in variance of sire expression over time be monitored, using techniques proposed by Sullivan (1999) to estimate heterogeneous variances.

The many differences in data recording and genetic evaluation systems among countries make it very difficult for Interbull to monitor and ensure consistent quality of national EBV from all countries. Emanuelson et al. (1999) discussed the impact of variation among national genetic evaluation systems on MACE results, concluding that increased harmonization of national methods would be desirable to increase the value of MACE results.

An alternative to MACE would be an international animal-model evaluation, eliminating the reliance on national EBV and enabling complete harmonization of evaluation models and methods across countries. Differences in climate, animal management, data recording practices and trait definitions among countries, however, make it impossible for one model and one trait definition to serve all countries equally well. Theoretically, each country could be treated as a separate trait, as is done in MACE, but this would result in MME of order equal to the number of countries times the number of international animals, approaching a billion equations for some biological and production traits of interest. The MME would be even larger if multiple production traits were to be evaluated simultaneously in a multiple trait and country evaluation, the number of equations being multiplied again by the number of traits per country. Parallel processing algorithms can be used to solve very large genetic evaluation systems more quickly (Larsen and Madsen, 1999; Madsen and Larsen, 1999), but computing costs and time would still be substantially greater than international evaluation strategies based on MACE.

Lohuis and Dekkers (1998) argued that defining traits by country and having separate data recording and evaluation systems among countries reduces the benefits of global selection because of artificially low genetic correlations between "country" traits. They suggested that traits should rather be defined by production environment. Such a system would be relatively more feasible if based on fewer production environments than there are countries, the order of the MME being reduced to the number of animals times the number of production environments. Weigel and Rekaya (2000) used a herd clustering approach as an attempt to develop such a model for dairy production traits.

Weigel et al. (2000) alternatively considered defining traits by region, but their results for goodness of fit and model parsimony favoured the trait-by-country model. Fikse et al. (2000) described a trait-by-country international animal model for Guernsey milk yield data, but found lower than expected heritabilities and suspected their model may have been incomplete with respect to the fixed effects included. They also suggested that the herd-clustering model should be considered in future work and that additional work is needed to include records beyond first lactation.

Recent attempts to evaluate dairy production traits with an international animal model have been restricted to a single production trait. These single-trait models would have to be repeated for each trait of interest and would fail to utilize information from correlated traits, for example milk and fat yields or milk yields in consecutive lactations. A multiple trait and country international animal model, or a multiple trait and production environment model may eventually become a reality, but for the Holstein breed could not encompass all traits of interest from all countries in the foreseeable future. Substantial work remains before international animal model evaluations will become a practical alternative to

MACE. There is considerable scope for combining multiple, sequentially-run international evaluations using MACE techniques.

VanRaden et al. (2000) presented a strategy to combine national evaluations from multiple countries within the framework of the animal model. The strategy is computationally much simpler than MACE, theoretically better than conversion strategies because it uses more information, and provides international evaluations for all animals including females. The strategy was recommended as a way to generate international evaluations for cows, but not to replace MACE for international evaluation of sires. The strategy could be used, however, as a computationally simpler alternative to MACE for simultaneously evaluating sires for multiple-traits in multiple countries.

2.3. Reliability of Genetic Evaluations

Estimates of breeding values (EBV) are point estimates. If the EBV are BLUP, they are unbiased in the sense that the expectations of the EBV are equal to the true breeding values (BV). The EBV are predicted with error, however, and the magnitude of the error depends on the amount of data available. The prediction error variance (PEV) of the EBV range from zero with infinite data to the true genetic variance when there are no data. The PEV can be computed from the diagonal elements of the inverse of the left-hand-sides (LHS) of the MME (Henderson, 1984).

The correlation between BV and EBV is also a function of the available data, and a direct function of the PEV. The square of the correlation, which is often referred to as reliability by dairy cattle breeders, is a commonly reported measure of the relative amount of data used to derive each EBV. Reliabilities of EBV are always positive, and approach a

maximum value of 1 for EBV that have an expected PEV near zero. The reliability is not affected by the observations themselves, but rather by the number of observations and how much information is contained in each observation that is relevant for predicting the EBV. The amount of information contained in each observation that is used for the EBV depends on the definitions and number of effects included in the model and also the second moments specified for the random effects. Reliabilities, like PEV, can be computed exactly from the inverse LHS of the MME, but many MME in animal breeding are of order greater than 1 million, and inversion of such large matrices is generally not feasible and rarely practical.

Procedures have therefore been developed to approximate EBV reliabilities. Meyer (1989) and Misztal and Wiggans (1988) derived procedures for single-trait animal models that were based on approximating diagonal elements of the inverse LHS by equation absorption techniques. These approaches were very efficient because of the sparse nature of the LHS. Koots et al. (1997) used selection index principles to approximate reliabilities, and Harris and Johnson (1998) also took advantage of selection index principles (Van Vleck, 1993) to approximate reliabilities in multiple trait models. Gengler and Misztal (1996), Graser and Tier (1997) and Jamrozik et al. (2000) have also proposed methods that could be used for multiple trait models. Strabel et al. (2001) proposed methods for multiple-trait models with maternal effects.

Reliability approximation methods in use today vary among countries because of the numerous techniques available, differences in data structure, evaluation models, and personal preferences of programmers in each country.

2.4. Weighting Factors in MACE

A notable feature of the MACE approach for international sire evaluation, as discussed in section 2.2 above, is the flexibility allowed for trait and model definitions in each participating country. Each national genetic evaluation model can be customized to best match the local trait definitions, production management and data recording systems. The starting point for MACE is an assumption that national EBV are the best genetic predictions possible from the independent data sets of each country. The EBV from the independent data sets are combined in a weighted fashion, based on the reliabilities of the EBV and the amount of genetic ancestry that is shared among countries. Weighting factors are used to account for the reliabilities of national EBV, such that higher weight is given to EBV with higher reliability.

As a first step in implementing MACE, number of daughters per sire was used as a weighting factor to account for varying amounts of information, and hence reliability, for the EBV of each sire in each country. Ideal weighting factors would also account for information loss in each national evaluation due to estimation of fixed effects, number and type of observations per daughter and differences in model definition relative to the MACE international model. Alternative weighting factors were studied by Fikse and Banos (1997, 1999a, 1999b, 2001) in attempts to account for these latter effects and new weighting factors for models that predict animal classification effects were recently implemented by Interbull (Interbull, 2000). Kistemaker and Sullivan (2000) and Strandén et al. (2000) extended the weighting factor definition of Interbull (2000) to include models that predict animal covariate effects, such as random regression animal test day models (Jamrozik et al., 1997; Reents and Dopp, 1996, 1997).

The derivation of the new weighting factors for MACE was based on the concept of effective information for the prediction of individual breeding values, which is also used in current methods of approximating reliabilities (Harris and Johnson, 1998; Koots et al., 1997; Jamrozik et al., 2000). National reliabilities could also be used to derive weighting factors for MACE (Sullivan et al., 1998), although comparisons of sires from different countries may be biased if there are differences in the reliability approximation procedures used by each country (Fikse and Sullivan, 1999).

In situations where reliability approximation procedures are similar for all countries, and comparable to the reliability approximations used in the weighting factor procedures of Interbull (2000), the approach of Sullivan et al. (1998) to compute MACE weighting factors is recommended. The latter approach can be implemented by the international evaluation agency, avoiding an extra computational step for each country wishing to participate in the international evaluation. Additionally, the reliabilities computed for the international EBV would be correctly aligned with the national reliabilities for every country, as discussed in Sullivan et al. (1998) and Fikse and Sullivan (1999).

2.5. Covariance Component Estimation for MACE

The BLUE and BLUP properties of MME solutions are subject to the assumption that variances and covariances of random effects are known without error. Accurate covariance estimates are therefore vital to obtaining optimal EBV with Henderson's MME. Henderson (1953) presented three procedures for variance component estimation, and these have gradually been replaced by newer procedures with better properties, as reviewed by Kennedy (1981a). The dominant procedures in animal breeding today are Restricted

Maximum Likelihood (REML) (Patterson and Thompson, 1971) and Bayesian analysis with Gibbs Sampling (Van Tassell and Van Vleck, 1996). Genetic relationships among all animals in the population under study are usually considered with either procedure.

The MACE model requires estimates of sire genetic variances and covariances among countries, which are the second moments of the random sire-by-country effects in the model. These parameters were originally estimated sequentially for all country pairs by approximation techniques (Schaeffer et al., 1996) and subsequently by REML for all countries simultaneously (Sigurdsson et al., 1996; Klei and Weigel, 1998). Schaeffer (2001) proposed a Gibbs sampling approach for MACE strategies that include multiple traits in multiple countries, and Sullivan (1998) proposed approximation techniques that could be used to estimate multiple genetic covariances simultaneously for all traits in all countries.

The number of covariance estimates needed is much larger with multiple than with single traits per country, and the traits considered for a single MACE analysis would generally be moderately or highly correlated. Covariance estimation methods for multiple traits and countries will therefore need to consider singular covariance matrices, because increasing the number of highly correlated traits increases the likelihood that the covariance matrix will be singular. Methods to estimate reduced-rank covariance matrices are available for this purpose (Elzo, 1996; Madsen et al., 2000).

Concerns that variance of sire expression may be heterogeneous over time (Cassandro et al., 1997; Miglior et al., 1998; Van Doormaal et al., 1999) led to the development of procedures by Sullivan (1999) that could estimate heterogeneous covariances, and exclude predicted breeding values that might be subject to selection bias. Interbull validated the procedures with simulated data (Fikse and Sullivan, 2000) and has

started using the procedures to monitor trends in sire variance over time for countries participating in their MACE evaluation service (Fikse, personal communications, 2000). Interbull is also considering an approach suggested by Miglior et al. (2001), which uses these procedures to base sire variance estimates on only recently born sires. Strategies for covariance component estimation for MACE will likely continue to evolve in the foreseeable future.

2.6. Genetic Groups

Application of genetic groups in applied animal evaluation systems has been a common practice (e.g. Redman et al., 1993; Golden et al., 1994; Pollak and Quaas, 1998; Sullivan et al., 1999). Kennedy (1981b) demonstrated the benefits of including genetic groups to decrease prediction errors, especially when selection has occurred and performance data or pedigree files are incomplete. These latter conditions are always expected, at least to some extent, in practice.

Genetic group effects for all individuals can be expressed as weighted averages of a smaller number of group effects, as described by Thompson (1979) for a sire model and by Westell (1984) and Robinson (1986) for an animal model. The MME for animal models with genetic group effects defined in this way were simplified by Westell et al. (1988), using a transformation technique that was described by Quaas and Pollak (1981) for sire models with genetic groups. These simplifications made it very easy to add genetic group effects, with very complex grouping definitions, to either sire or animal models. Quaas (1988) warned of problems due to potential confounding between group and other fixed effects in the model, primarily because of the ease in implementing models with complex genetic

group definitions. Sullivan (1995) expanded on these concerns as they relate to potentially high degrees of singularity in the MME when genetic groups are treated as fixed effects in the model, even with simple group definitions.

An alternative to avoid singularity, proposed by Schaeffer and Kennedy (personal communications, 1990) is to add a constant to the diagonals of the group equations in the MME, effectively treating group effects as random. Sullivan and Schaeffer (1994) demonstrated both computational and prediction accuracy advantages of the groups-random approach, and Schaeffer (1994) proposed the groups-random approach for his MACE model.

Sullivan (1995) compared genetic groups models with uncertain parentage models (Henderson, 1988; Famula, 1992; Perez-Enciso and Fernando, 1992) and showed that by adding certain constants to the group equations, these two classes of models would produce identical results for predictions of animal breeding values. The groups-random approach proposed by Schaeffer (1994) is intermediate to the groups-fixed and uncertain parentage approaches, and much closer to groups-fixed than to uncertain parentage, especially if the numbers of unknown parents per group is large.

2.7. Connectedness

Genetic evaluations are used to compare individuals for their relative breeding values. When comparing individuals from different countries, or other definable sub-populations, predicted differences between the individuals include predictions of the average genetic differences between the sub-populations. There may also be environmental differences, however, affecting performance in each sub-population and the evaluation

model must therefore partition the observed differences in performance into average environmental and genetic effects for each sub-population.

Genetic connections between the sub-populations are required in order to separate the genetic and environmental portions of the performance differences between the sub-populations. The term connectedness refers to the number and quality of these genetic connections. Kennedy and Trus (1993) reviewed the concepts of connectedness and the implications for genetic evaluation, describing situations where sub-population genetic differences would not be estimable or would have high variance of prediction error (PEV). The authors gave special attention to models with genetic groups, since connectedness is particularly important with those models. Hanocq et al. (1996) also found important effects of connectedness on PEV of genetic differences between sub-populations. Connectedness varies among countries and populations (e.g. Banos et al., 1991; Klei and Lawlor, 2001; Weigel et al., 2001) and may be of practical concern for PEV of genetic differences between countries in international evaluations.

Connectedness would also affect the accuracy of covariance component estimates. Schaeffer (1975) suggested that only well-connected data subsets should be used to estimate genetic variances, but Eccleston (1978) rebutted with a proof that all data should always be used. Sigurdsson and Banos (1995a), however, showed that with international data undergoing selection within and across countries, the use of all data resulted in biased estimates of genetic correlations between countries for MACE, while the use of a well connected data subset gave unbiased estimates. The importance of connectedness clearly depends on the evaluation model being used and the characteristics of the data being evaluated. Connectedness is most important when genetic and environmental factors in the

model are confounded unless there are genetic connections between the sub-populations, and when data are undergoing selection forces that may not be fully accounted for by the model.

2.8. Selection

Schaeffer et al. (1998) reviewed statistical methods that have been proposed in the literature to account for selection and minimize selection biases in genetic evaluations. Some examples of selection forces that may cause problems in genetic evaluation were:

“... non-random selection and mating of breeding animals (parental selection), sequential selection, culling of animals before records are official, preferential treatment, selective reporting, and misclassification or manipulation of contemporary groups.”

Statistical methods were not found that could consistently and effectively account for most of these selection forces, particularly because information about these factors would not typically be available from the data available for genetic evaluation.

Henderson (1984) and Sorensen and Kennedy (1984) demonstrated the effectiveness of the MME in accounting for certain types of selection, provided that all observations and pedigrees related to the selection that occurred were used to form the MME. The addition of genetic groups to the model has been suggested to reduce problems of selection bias when pedigree data are not complete (Sorensen and Kennedy, 1984; Westell et al., 1988; Sullivan, 1995). Genetic groups account for differences in

sub-population means due to selection, but not for changes in genetic variances or higher moments within sub-populations. For example, selection effects on the variance of Mendelian sampling effects due to selective reporting of data are not accounted for by the inclusion of genetic groups in the model (Quaas, 1988).

Genetic groups should theoretically be treated as fixed effects to account for selection effects on sub-population means. If genetic comparisons of interest are non-estimable with fixed group effects, however, it may be necessary to treat groups as random effects or redefine groups in a sub-optimal way to avoid the problems created by the desired group definition. The effectiveness of random genetic group effects, in accounting for selection effects associated with missing data or pedigree information, has not been established.

2.9. Inbreeding

Covariances between genetic effects of different animals, and between independently sampled genetic effects for the same animal, are accounted for in the MME with the use of an inverse of the animal relationship matrix (A^{-1}). Increased covariances within and between animals due to inbreeding are accounted for in A^{-1} . The A^{-1} matrix can be formed from animal pedigrees using rules presented by Henderson (1975a) when sires and dams are identified in the pedigrees, or Henderson (1975c) when the pedigrees are based on sires and maternal grandsires only. Inbreeding levels of individual animals are accounted for in Henderson's rules to form A^{-1} , but computational demands are much larger when accounting for inbreeding. A computational step can be eliminated by assuming that all animals are non-inbred.

Quaas (1976) described an algorithm to simplify the computations that relate to inbreeding, but inbreeding is often ignored in practice, as for example in the procedures of Schaeffer and Kennedy (1986). Inbreeding is ignored in the A^{-1} matrix used for MACE, as currently applied by Interbull for international dairy sire evaluations. Mehrabani-Yeganeh et al. (2000) investigated the validity of ignoring inbreeding for genetic evaluation, by measuring responses to selection in simulated populations with very high levels of inbreeding. They found no differences in responses to selection based on estimated breeding values from MME, whether or not inbreeding was considered for the construction of A^{-1} .

2.10. Summary

Genetic evaluation strategies have evolved with increasing computer power. Early models of evaluation were based on sire effects (sire models) to limit the number of individuals evaluated to sires only, thereby reducing computing requirements. Evaluations were also limited to a single trait to reduce computing requirements. Faster computers with larger amounts of memory, coupled with advances in computing strategies, enabled applications of better models to predict effects for all animals (animal models), to account for known genetic relationships among all animals, and to evaluate multiple traits simultaneously. These more complex models are believed to produce more accurate predictions of animal breeding values (EBV) and to be less affected by selection biases. Multiple-trait animal model evaluations are common today within a country, but the computational demands of international animal models can still exceed the limits of today's computers.

International genetic evaluations of dairy sires are routinely computed for production, conformation and udder health traits, using a multiple-trait across country evaluation (MACE) strategy. The MACE strategy employs a model that describes national genetic evaluations of sires rather than phenotypic observations. A sire model is used in MACE, but the input evaluations are typically computed from national animal model systems. Weighting factors are used to account for differences in reliability of the national sire evaluations, and a deregression procedure is used to account for covariances among the input evaluations of genetically related sires. The weighting factors and deregression procedures assume incorrectly, however, that all national sire evaluations were derived from single-trait evaluation systems. This thesis will investigate a number of alternative weighting factor and deregression approaches to account for the multiple-trait nature of many of today's national evaluation systems. An international (global) animal model system (GAM) that simultaneously evaluates multiple traits in multiple countries may become feasible in the future, and will also be considered in this thesis.

Monte Carlo simulation will be used to create data sets to evaluate with the various international evaluation strategies. True genetic values of individuals will therefore be known. The thesis will consider the effects of selection within and among countries, both before and during the time period when data are recorded, the direction of gene flow and the degree of genetic connectedness among countries. Inbreeding will be ignored in genetic evaluation, and therefore minimized in the simulated data. True variances and covariances will be used for the evaluation strategies to reduce the computing requirements of the study. The implications of using estimated parameters in practice, however, will be discussed. Genetic group effects will be included in all strategies and the implications of treating

groups as random or fixed effects will be discussed. Special attention will be devoted to genetic group effects in chapter 4.

3. TRADITIONAL GENETIC EVALUATION STRATEGIES

Methods based on traditional MME, which have been used or proposed as genetic evaluation strategies to compare sires internationally, are considered in this section of the thesis. Strategies based on MME with modifications to account for selection will be considered in Chapter 4.

The traditional strategies that were considered, to compute international genetic evaluations on the scales of all countries for all sires, can be grouped into three categories. The first two categories required two steps, the first step being a national genetic evaluation by each country and the second step being a method to derive international evaluations from the available national evaluations. The national animal model (NAM) strategy provided genetic evaluations for a different subset of sires for each country, and can be compared to international strategies for sire comparisons that are restricted to the subsets of sires nationally evaluated in each country. International comparisons of interest, however, often extend beyond those subsets of sires.

The first category of strategies (CNV) for international evaluations relied solely on the national EBV from each sire's country of birth, using linear conversion formulas to predict genetic expression on the scale of each foreign country. The converted EBV ranked sires from one country identically on the scales of all other countries. For sires used internationally, national EBV in countries other than the sire's country of birth were ignored with the CNV strategies. International evaluation strategies would generally use performance information or genetic evaluations from all countries where a sire has progeny.

The CNV strategies therefore represented controls relative to all of the international evaluation strategies.

The second category of strategies used MACE to combine information available from all national sire EBV from each country, including EBV from multiple countries for sires that were used internationally. With these strategies, sires could re-rank across countries of evaluation. The MACE procedure of Schaeffer et al. (1996) required modification to accommodate multiple-trait national EBV, and several alternative modifications were considered, including the proposal of Schaeffer (2001).

The third category of strategies, involving only one step, was a global animal model (GAM) evaluation for all animals, ignoring the national EBV that were available for sires. The GAM allowed for re-ranking of all animals, was theoretically the best strategy, and is the strategy that MACE was originally designed to approximate. All strategies are outlined in Table 1.

The true genetic variances and covariances, which will be described in the data simulation section of the thesis, were used as needed for each of the genetic evaluation strategies. The inverse of the animal relationship matrix (A^{-1}), which was required to account for covariances between animal effects in the MME used with each strategy, was formed by ignoring inbreeding (Henderson, 1975a, 1975c).

Table 1. Genetic evaluation strategies.

One (index) trait evaluated per country

CNV1	Convert index on scale of birth country to index on scale of each foreign country
STn	Combine available sire indexes from all countries using single-trait MACE, with numbers of daughters as weighting factors
STe	Combine available sire indexes from all countries using single-trait MACE, with effective daughter contributions to the index (Interbull, 2000) as weighting factors

Three (lactation) traits evaluated per country

CNV2	Convert lactation evaluations from birth country to lactation evaluations on the scale of each foreign country
NAM	Use local (national) evaluations, ignoring foreign bulls since NAM evaluations are only available for local and imported bulls
RSn	Repeated single-trait MACE analyses to compute multiple-country evaluations, one lactation trait at a time, with numbers of daughter lactation records as weighting factors
RSe	Repeated single-trait MACE analyses to compute multiple-country evaluations, one lactation trait at a time, with effective daughter contributions (Interbull, 2000) for each lactation as weighting factors
MTr	Multiple-trait MACE of all lactation traits in all countries, with weighting blocks taken from $Z'R^{-1}Z$ (Schaeffer, 2000)
MTn	Multiple-trait MACE of all lactation traits in all countries, with numbers of daughter lactation records as weighting factors (i.e. ignore residual correlations between lactations when forming $Z'R^{-1}Z$)
MTe	Multiple-trait MACE of all lactation traits in all countries, with effective daughter contributions (Interbull, 2000) for each lactation as weighting factors
MTi	Multiple-trait MACE of all lactation traits in all countries, with effective independent daughter lactation records (Appendix 2) as weighting factors
GAM	Global animal model of all lactation traits in all countries, using complete pedigree and cow performance data bases

3.1. National Strategy

A multiple-trait national animal model strategy (NAM) was applied to all locally recorded first, second and third lactation records of cows, using all known pedigrees back to the base generation animals that had unknown ancestry. All data used for selection were not included, however, because each country used sires from foreign countries in their breeding programs, and the foreign country performance data, which were used to identify superior foreign sires, were not included in the local evaluation. Genetic groups were therefore included in NAM to account for selection of foreign sires, and to match the common practice of countries applying NAM strategies for dairy production traits (Interbull, 2001a).

Genetic groups were defined by the four grandparent paths of selection (Rendel and Robertson, 1950) and by country of progeny's birth. Year of birth was not part of the group definition because all pedigrees were complete back to year 0. Genetic group effects were treated as random. Variances and covariances among traits within each group were arbitrarily assumed equal to the variances and covariances among traits for a non-inbred animal and covariances between groups were assumed equal to zero (Sullivan and Schaeffer, 1994).

3.2. Conversion Strategies

Lactation evaluations in a given country were combined into an index that was used as a selection criterion. The indexes were different for each country, and are fully described in section 3.5.1.4. Indexes were computed by country, for each local sire, using NAM evaluations for the lactation traits. The indexes were converted to the scales of foreign

countries with strategy CNV1. Strategy CNV2 was to convert each lactation evaluation, and then combine the converted lactation evaluations into the index, on the scale of each foreign country. Therefore, strategy CNV1 involved conversions of one trait per country, whereas CNV2 involved conversions of three traits per country.

The conversion strategies required an intercept and linear regression term for each conversion equation. The intercepts for each pair of countries were estimated from the simulated data by computing the paired means of national EBV for all sires that had national EBV on the scales of both countries. The intercept for the conversion of EBV from the scale of country X to the scale of country Y, for example, was the mean EBV on scale Y minus the mean EBV on scale X. The regression terms were derived from the true genetic variances and covariances among countries, for the index or lactation trait being converted. Conversion equations were therefore reciprocal and as close as theoretically possible to the best conversion equations that might be estimated in practice.

3.3. MACE Strategies

The MACE strategies were all structured around the general form of the MME under a sire model, which can be described as follows with fixed effect equations absorbed into the equations for random sire effects ($\mathbf{u}$):

$$[\mathbf{Z}'\mathbf{M}\mathbf{Z} + \mathbf{G}^{-1}][\mathbf{u}] = [\mathbf{Z}'\mathbf{M}\mathbf{y}],$$

$$\mathbf{M} = \mathbf{R}^{-1} - \mathbf{R}^{-1}\mathbf{X}(\mathbf{X}'\mathbf{R}^{-1}\mathbf{X})\mathbf{X}'\mathbf{R}^{-1}$$

where $\mathbf{G}$ and $\mathbf{R}$ are covariance matrices of random and residual effects, respectively, $\mathbf{X}$ and $\mathbf{Z}$ are design matrices linking observations in $\mathbf{y}$ to fixed and random effects, respectively,

and $\mathbf{u}$ is a vector of random effects. When $\mathbf{R}$ is an identity matrix times a scalar σ^2 , these equations can be simplified by multiplying each row by σ^2 to form:

$$[\mathbf{Z}'\mathbf{N}\mathbf{Z} + \mathbf{G}^{-1}\sigma^2][\mathbf{u}] = [\mathbf{Z}'\mathbf{N}\mathbf{y}],$$

$$\mathbf{N} = \mathbf{I} - \mathbf{X}(\mathbf{X}'\mathbf{X})^{-1}\mathbf{X}'$$

The left-hand-side (LHS) of either form of the MME can be thought of as containing two components. The first component ($\mathbf{Z}'\mathbf{M}\mathbf{Z}$) is the records portion and is equal to the sum of inverse residual covariances for each record combination observed, times the number of occurrences of each combination, adjusted for the estimation of fixed effects. Under a single-trait sire model with no fixed effects, this would equal the number of progeny observations times the inverse of the residual variance for $\mathbf{Z}'\mathbf{M}\mathbf{Z}$, or simply the number of progeny observations for $\mathbf{Z}'\mathbf{N}\mathbf{Z}$. Weighting factors multiplied by the residual variance are used in place of $\mathbf{Z}'\mathbf{M}\mathbf{Z}$ for MACE.

The second component of the LHS is the covariance portion, and is equal to the inverse of the covariance matrix among levels of $\mathbf{u}$. Taking $\mathbf{u}$ to contain only sire effects, the covariance portion is a function of the genetic relationship matrix ($\mathbf{A}$) among the sires and genetic groups being evaluated and the underlying genetic covariances ($\mathbf{G}_{(t)}$) among the observed t traits ($\mathbf{G} = \mathbf{A} \otimes \mathbf{G}_{(t)}$). For a single-trait within-country evaluation, the univariate case, $\mathbf{G}_{(1)}$ is a scalar. For the multivariate case, with multiple traits and/or countries, $\mathbf{G}_{(t)}$ is a matrix.

The first step in MACE is to re-compute $\mathbf{Z}'\mathbf{N}\mathbf{y}$ for each country by multiplying an approximation of the original LHS with the matrix of within-country genetic evaluations ($\mathbf{u}$). This computation is commonly referred to as the de-regression step (Sigurdsson and Banos, 1995b; Rozzi and Schaeffer, 1996; Jairath et al., 1998). The deregression step

produces the right-hand-side of a sire model MME that would yield the same sire evaluations that were provided by the country, regardless of the national evaluation model that was used. For example, the country may have used a single-trait or multiple-trait animal model rather than a single-trait sire model in their national genetic evaluation system. The approximate LHS used is the sum of the approximations of $\mathbf{Z}'\mathbf{N}\mathbf{Z}$ and $\mathbf{A}^{-1}$ times the ratio of residual and genetic variances for the country. The next step in MACE is to estimate $\mathbf{G}_{(i)}$ and $\mathbf{R}$ for use in a multivariate analysis across countries. The final step is to rebuild and solve the MME under the formulation that involves matrix $\mathbf{M}$.

Existing applications of MACE are based on a simplified model that assumes single-trait national EBV are being used. When national EBV are from a multiple-trait system with non-zero genetic and residual correlations among traits, the records portion of the MME becomes block-diagonal and the MME formulation involving $\mathbf{M}$ must be used instead of the formulation involving $\mathbf{N}$. A weighting block is then required, theoretically, instead of a weighting factor for each nationally evaluated sire.

The diagonal blocks of $\mathbf{Z}'\mathbf{M}\mathbf{Z}$ could be computed exactly for all sires, and used in MACE, but likely with little computational advantage over an international animal-model strategy. Simpler alternatives were therefore considered, including two single-trait MACE (ST) and six multiple-trait MACE (MT) strategies (Table 1).

The current practice of Interbull is to allow only one trait per country and to apply ST one trait at a time. In the case of production traits, the trait provided to Interbull by some countries is a linear combination (single index) of the multiple traits that were evaluated nationally. In the present study, each country provided the index that was used as their selection criterion and these indexes were included in ST analyses using two alternative sets

of weighting factors. The STn and STe strategies represent the previous and current strategies of Interbull for the traits of milk, fat and protein yield, for countries that produce lactation-specific evaluations nationally (e.g. Canada, Germany, Finland and the Netherlands).

As an alternative to using ST with the indexes, evaluations for each lactation trait could be provided by all countries, and repeated ST analyses (RS) could be performed one lactation trait at a time. The MACE solutions for each lactation trait in each country are then combined using the linear index equations of each country. The RS approach would only be useful when all countries have the same set of multiple-traits of interest, but was of theoretical interest for the present study. The RS approach was applied in the present study using two alternative sets of weighting factors.

The multiple-trait MACE (MT) approach comes with a larger number of possibilities for weighting factors, since it involves matrices instead of scalars for each sire. Schaeffer (1999 and 2001) was the first to propose a complete MT model, using as weighting matrices the sire diagonal blocks of $\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}$ under a national sire model. The choice of $\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}$ was a simple approximation to $\mathbf{Z}'\mathbf{M}\mathbf{Z}$. Better approximations of $\mathbf{Z}'\mathbf{M}\mathbf{Z}$ would generally be more difficult to compute, which could negate the computational benefits of MACE over a GAM strategy.

Alternative weighting factors suggested by Fikse and Banos (2001) have been regarded as improvements over factors that are based on $\mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}$ for single-trait MACE, but are not directly applicable to the multiple-trait procedures of Schaeffer (2001). Multiple-trait MACE strategies that could be easily implemented by Interbull were of particular interest. Therefore, multiple-trait MACE strategy alternatives were considered in addition

to the strategy of Schaeffer (2001). The approach of Schaeffer (2001) was the only MACE strategy considered in the present study that used weighting matrices instead of scalar weighting factors for each sire.

The MT strategies that were based on scalar weighting factors, by trait, were derived from data that are already provided to Interbull, by participating countries, or have been described by Interbull. Two of these alternatives (MTn and MTe) used the same weighting factors that were considered for the RS approaches, and would be the simplest to implement by Interbull member countries and by Interbull. The final MT alternative was based on a theoretical adjustment to the weighting factors from RSe to account for equation differences between RS and MT, with respect to G^{-1} . The weighting factors in RSe account for the fact that the RS equations ignore genetic correlations among lactation traits. The MT equations, by contrast, incorporate genetic correlations among lactation traits, so the RSe weighting factors were adjusted to account for this difference, deriving effective independent daughter lactation records (Appendix 2), for the MTi approach.

Genetic groups were used in all MACE strategies, using the same group definitions in all cases. Genetic groups were defined by path of selection, and by country and year of birth of progeny, equivalent to the group definition used by Interbull (Banos and Sigurdsson, 1996). Paths of selection were sire, maternal grandsire and maternal granddam of sire. Sires were identified back to year 0, but maternal grandparents had progeny in years greater than 0. Genetic group effects were treated as random. Variances and covariances among traits within each group were arbitrarily assumed equal to the variances and covariances among traits for a non-inbred sire and covariances between groups were assumed equal to zero (Sullivan and Schaeffer, 1994).

3.4. Global Animal Model Strategy

The global animal model (GAM) strategy was applied to performance data of cows, for the three lactation traits in each country, in a simultaneous 12-trait analysis. Pedigree data were complete back to base generation animals that had unknown ancestry. In contrast to NAM, all data used for selection after year 0 were included in the GAM analyses. Genetic groups were nevertheless included in the GAM strategy, as would likely occur if GAM were applied in practice.

Genetic groups were defined by the four grandparent paths of selection (Rendel and Robertson, 1950) and by country of progeny's birth. Year of birth was not part of the group definition because all pedigrees were complete back to year 0. Genetic group effects were treated as random. Variances and covariances among traits within each group were arbitrarily assumed equal to the variances and covariances among traits for a non-inbred animal and covariances between groups were assumed equal to zero (Sullivan and Schaeffer, 1994).

3.5. Materials and Methods

3.5.1. Data Simulation

3.5.1.1 Multiple Traits and Populations

Data were simulated to create a separate population of animals in each of four countries. Three correlated traits were measured and evaluated in each country. All traits were also correlated across countries. Genetic correlations among the traits were moderate

to high, both within and among countries (Table 2). Genetic variances for each trait were equal to one and are unit-less, representing traits that are variance-standardized. Genetic correlations were what may be typically expected among milk, fat and protein yields of dairy cattle, or first, second and third lactation traits for milk, fat or protein yield. Residual correlations were half the value of the corresponding genetic correlations, similar to correlations that have been estimated for dairy production traits across lactations in Canada (Jamrozik, personal communications, 1999). Heritability was assumed to be moderate (30%) for each of the three traits.

Table 2. Genetic correlations among lactation traits within and across countries.

Country	Trait	EXP1			EXP2			IMP1			IMP2		
		1	2	3	1	2	3	1	2	3	1	2	3
EXP1	1	1.0	0.8	0.7	0.9	0.7	0.6	0.9	0.7	0.6	0.9	0.7	0.6
	2	0.8	1.0	0.9	0.7	0.9	0.8	0.7	0.9	0.8	0.7	0.9	0.8
	3	0.7	0.9	1.0	0.6	0.8	0.9	0.6	0.8	0.9	0.6	0.8	0.9
EXP2	1	0.9	0.7	0.6	1.0	0.8	0.7	0.9	0.7	0.6	0.9	0.7	0.6
	2	0.7	0.9	0.8	0.8	1.0	0.9	0.7	0.9	0.8	0.7	0.9	0.8
	3	0.6	0.8	0.9	0.7	0.9	1.0	0.6	0.8	0.9	0.6	0.8	0.9
IMP1	1	0.9	0.7	0.6	0.9	0.7	0.6	1.0	0.8	0.7	0.9	0.7	0.6
	2	0.7	0.9	0.8	0.7	0.9	0.8	0.8	1.0	0.9	0.7	0.9	0.8
	3	0.6	0.8	0.9	0.6	0.8	0.9	0.7	0.9	1.0	0.6	0.8	0.9
IMP2	1	0.9	0.7	0.6	0.9	0.7	0.6	0.9	0.7	0.6	1.0	0.8	0.7
	2	0.7	0.9	0.8	0.7	0.9	0.8	0.7	0.9	0.8	0.8	1.0	0.9
	3	0.6	0.8	0.9	0.6	0.8	0.9	0.6	0.8	0.9	0.7	0.9	1.0

A multiple-trait evaluation system becomes equivalent to multiple single-trait evaluation systems as correlations among traits go to zero. The focus of the present study was on the value of multiple-trait evaluation alternatives, particularly in relation to multiple

single-trait evaluation systems. The benefits of using a multiple-trait approach are quickly reduced as correlations among traits approach zero, so lowly correlated traits were of little interest for the present study.

The populations were treated as if separated by country boundaries, but could also represent populations distinguished for example by region, production environment, breed or genetic line. All matings were by artificial insemination (AI) and all genetic exchange among countries was through sales of semen. Two countries were exporters and two were importers. The exporters marketed semen to each other and to the importers, and the importers did not market semen outside their own country. Each country contained herds of cows, each herd of equal size and age distribution, plus one AI stud that owned all bulls available for breeding. One exporting country was twice the size of each of the other three countries, which were of equal size in terms of numbers of herds and bulls. The number of bulls in each AI stud was directly related to the number of herds and hence the size of the cow population.

3.5.1.2. Females

The cow segment of each population was divided among either 200 or 100 herds, each herd containing 30 milking cows, plus calves and yearling heifers. Age distribution of the cows within a herd remained constant throughout the simulation. First lactation production started when cows were two years of age, and subsequent lactations started at annual intervals. The numbers of cows in first up to a maximum of seventh lactation were 10, 7, 5, 3, 2, 2, and 1, based on the average age distribution in Canadian Holstein herds

(Collard et al., 1999). The three traits simulated for each country were representative of lactation-specific production yields of dairy cattle.

One trait was simulated per lactation and could be considered representative of milk yield, protein yield, fat yield or a combination of yield traits. Culling of cows was based on phenotypic yield in the most recent lactation, with the lowest yielding cows being culled. Ten female progeny of the 30 lactating cows in the herd were randomly chosen to survive to first lactation at two years of age, replacing the ten cows that were culled each year. All culling prior to two years of age was therefore involuntary, while all culling at older ages was voluntary. Combinations of involuntary and voluntary culling could be simulated at all ages, in future simulations, with the use of culling variables that have correlations less than unity with genotypes and/or phenotypes (Jansen, personal communications, 2002).

3.5.1.3. Males

The bull segment of each population was maintained in the AI stud. Bull calves that were not selected by the AI stud were culled from the herd as calves. The AI stud managed three categories of bulls:

1. "Young" bulls chosen for random sample matings and preliminary evaluation.
2. "Shelved" bulls that have completed their sample mating period, but whose daughters have not yet completed their first lactation production records. Semen is regularly drawn from these bulls and stored (shelved) for potential future use, but is not used unless and until the bull is selected as a proven bull.

3. "Proven" bulls that are selected each year based on the most recent national evaluations.

All bull selection decisions were based on a population-specific selection criterion using EBV from each of three lactations, as described below.

3.5.1.4. Selection and Mating

National EBV were computed each year for the three lactation traits, separately by each country. The national EBV were used to derive selection criteria to compare proven bulls within each of two distinct groups, those with local EBV and those without local EBV. Comparisons between the two groups were not made within the simulation, as will become clear by the end of this section. For the latter group of bulls, which were proven in foreign countries but not locally, the EBV from the bull's country of birth were used in place of the missing local EBV. Genetic correlations of unity, between the corresponding lactation traits in the foreign and local countries, were implicitly assumed by this approach. International EBV were not computed within the simulation, and therefore not used for any selection decisions, but were run afterwards on the completed data sets to compare alternative evaluation strategies.

The national EBV for each lactation were combined in a country-specific linear index of overall merit, to be used as the criterion for selection within the country. The weightings in the index for the first importing country were similar to the weightings for the first exporting country. The weightings were also similar for the second importer relative to

the second exporter, but different from the weightings for the first importer and exporter. The index weightings for each country were as follows;

Exporter EXP1: [0.60 0.30 0.10]

Importer IMP1: [0.75 0.25 0.00]

Exporter EXP2: [0.33 0.33 0.33]

Importer IMP2: [0.30 0.40 0.30]

The smaller exporter EXP2, and importer IMP2, selected for a balance of superiority across all three lactations, whereas the larger exporter EXP1, and importer IMP1, selected more heavily for production in early life. Differences in selection criteria were expected to affect the levels of semen exchange among the various pairs of countries, as might happen in practice when groups of countries have different breeding objectives. The breeding objectives for each country were weighted averages of the true BV for each trait, using the same weightings above that were used to weight the EBV for the selection criteria.

Bull calves selected in each country were the result of assortative matings of elite bulls with elite cows. The top two cows in each herd, based on the selection criterion for the country, were mated to a bull from the top 50% of bulls in the proven bull line-up. Sex of calf was determined by chance with equal probability of being male or female. The best male progeny from the elite matings, based on the average selection criterion value of parents, were selected by the AI stud to be sample-mated to the cow population as yearlings.

The selected yearling bulls were mated to cows drawn randomly from randomly chosen herds, to create 20 daughters per bull that would survive to the end of first lactation. In practice, young bulls may be mated to more cows than was simulated, because of uncertainty that progeny would be female and survive to first lactation, and because daughters may be non-randomly distributed across herds and production environments. The simulation approach, however, offered a guaranteed number of daughters with production records and a random distribution of those daughters across herds. Minimum reliabilities of approximately 60% were achieved for EBV of young bulls based on 20 "first-crop" daughters completing first-lactation production. Semen collection continued for young bulls, but the semen was "shelved" until the bulls received their first genetic evaluation after their first-crop daughters completed first-lactation production. The "young bulls" with the best national genetic evaluations competed with previously proven bulls in the AI stud for a place in the "proven bull" line-up, which had a limited number of spaces.

Each year, the bulls in the proven bull line-up from the previous year, and the imported foreign and local young bulls that received their first local proof, were ranked by the selection criterion. The top bulls from the sorted list were chosen as part of the next proven bull line-up, leaving some spaces at the bottom of the list for new foreign bulls not yet proven locally. The foreign bulls added to the bottom of the line-up were shelved after one year of use until they received their first local "second-country" proof, at which time they competed with the proven and young local bulls for a spot in the top section of the proven bull line-up. The selection criterion used to identify foreign bulls for the bottom section of the proven bull line-up was computed by combining foreign-scale EBV with the local-scale index weightings.

The number of spaces for foreign bulls was varied to study the impact of different levels of semen exchange among the populations. Whereas the number of locally proven foreign bulls used was variable, depending on the relative genetic superiorities among countries, the number of foreign bulls initially sampled each year was held constant to guarantee a continuous use of foreign bulls in all countries. Similarly, a maximum was imposed for the number of locally proven foreign bulls in the line-up to guarantee a continuously high proportional use of local bulls in all countries. These constraints created proportions of foreign bulls in proven bull line-ups that could range from 0.067 to 0.133 with low semen exchange, 0.167 to 0.250 with moderate semen exchange, and 0.200 to 0.400 with high semen exchange.

A mating probability vector was created to allocate higher probabilities of use for the better bulls in the proven bull line-up (bulls higher in the list). Mating probability (MP_i) for the i^{th} of n bulls was defined as follows:

$$MP_i = [4/(3n)] * [1 - (i-1)/(2n-2)], \quad i=1,n$$

The above equation satisfies the requirements of a probability distribution function (Freund, 1992), and guarantees a linear decrease in probability from a maximum that is equal to twice the minimum. The derivation of the equation is in Appendix I. Average matings to the proven bulls with highest to lowest probabilities of mating were, respectively, 3.11 and 1.56 times the number of matings for young bulls.

Matings of proven bulls to closely related cows were avoided as much as possible by limiting the number and type of common ancestors among parents and grandparents of the offspring of potential matings. This restriction was used to minimize the amount of

inbreeding in the populations of animals to be evaluated, and therefore minimize the impacts of ignoring inbreeding with each of the genetic evaluation strategies.

3.5.1.5. Breeding Values and Phenotypes

True genetic values of animals were simulated as averages of parental values for each trait in each country plus random Mendelian sampling (MS) terms. The MS terms were within-family genetic deviations, and were distributed multivariate normally across the 12 traits-by-country. Zeroes were assumed for parental values when parents were unknown, and the random deviations (MS) were then distributed as follows:

$$E(\mathbf{MS}) = \mathbf{0}$$

$$V(\mathbf{MS}) = \begin{cases} \mathbf{G}_{(12)} & , \text{ parents unknown} \\ (.5 - .25(F_{sire} + F_{dam}))\mathbf{G}_{(12)} & , \text{ parents known} \end{cases}$$

The matrix $\mathbf{G}_{(12)}$ was described in Table 2. The term F_i is the coefficient of inbreeding for individual i , and represents the probability that both genes in a pair in the individual's genotype, one from the individual's sire and the other from the dam, were identical by descent. Inbreeding coefficients were computed as animals were created using the approach suggested by VanRaden and Hoeshele (1990), which was to build a relationship matrix for all animals in the recorded ancestry of the particular animal and derive the inbreeding coefficient from the relationship between the animal's sire and dam.

Phenotypic records were simulated for the first three lactations by adding correlated residual terms to the cow's genetic value for each lactation. Correlated genetic and residual terms were each derived by independently simulating a vector of random normal deviates ($\mathbf{w} \sim \text{MVN}(\mathbf{0}, \mathbf{I})$), and then pre-multiplying by a lower triangular matrix ($\mathbf{L}$) which

was the Cholesky decomposition of the desired correlation matrix. For example, for the genetic terms:

$$\begin{aligned} \mathbf{G}_{(12)} &= \mathbf{L}\mathbf{L}' \\ \mathbf{V}(\mathbf{L}\mathbf{w}) &= \mathbf{L}\mathbf{V}(\mathbf{w})\mathbf{L}' \\ &= \mathbf{L}\mathbf{L}' \\ &= \mathbf{G}_{(12)} \end{aligned}$$

Phenotypic records beyond third lactation were weighted averages of the previous phenotypic record and a simulated phenotypic deviation. Weights were from a Cholesky-decomposed phenotypic correlation matrix of order two, assuming phenotypic correlations of 0.75 between all consecutive lactations beyond the third.

3.5.1.6. Selection in Base Generation Populations

Selection was simulated in base generation populations to mimic the situation where base generation males are genetically above the mean and exporting countries have higher genetic means than importing countries. Above average genetic values were simulated for base generation males, in all countries, from truncated normal distributions, and different means were added to the genetic values of all individuals, male and female, by country. The selection in base populations violates basic assumptions for the MME, and was relaxed in a control simulation that had unselected base populations. With unselected base populations genetic values of males were sampled from complete normal distributions and all country means were set to zero.

With selected base populations, base generation males were above average for the selection criterion of their country of birth, assuming that above average bulls could have

been identified prior to the establishment of formal performance recording and genetic evaluation programs. Base generation males included proven bulls and unproven young bulls already chosen for sampling in year 1 of the simulation. Genetic values of males were generated by re-sampling from complete normal distributions until the selection criterion was met.

Genetic means for all traits in all countries, with selected base populations, were 0 in exporting countries and -1 in importing countries, assuming that the exporting countries had been able to achieve a level of genetic superiority over the importing countries in both the male and female populations.

In all simulations, base generation males and females were unrelated within and among countries and base generation females were unselected.

3.5.1.7. Simulation Overview

The steps involved for each simulation are outlined in Figure 1. Base generation populations were the bull and cow populations that were simulated in year 0 (***SIMULATE BASE***). Base generation cow populations included cows 2 years of age and older that would be lactating during year 0, and also future replacement heifers that would replace the cows culled at the end of year 0. Similarly, base generation bull populations included proven, shelved and young bulls plus the calves that would have already been selected for progeny-testing in year 1.

Within each year of the simulation, the first step was to breed all cows and yearling heifers to available AI bulls (***MATE***). Elite cows and bulls were mated to create a pool of male progeny from which to draw bull calves for future progeny-testing. Young bulls

Figure 1. Simulation flow chart.

that were previously identified for progeny-testing were then randomly mated to cows not yet bred. The remaining cows, which were not mated either to elite or young bulls, were mated to proven bulls. Performance records of cows were then simulated for the current year (*LACTATE*), and a national animal model genetic evaluation was performed for each country (*EVALUATE*). The results from the genetic evaluation were used for selection and mating decisions of the following year, and cows were culled within each herd (*CULL*).

3.5.1.8. Replications and Data Summary

Each simulation was run for 15 years and replicated 20 times. The same set of 20 different starting seeds was used for each of the different simulations. Unless otherwise stated, all results are reported as the mean $\pm$ the standard error ($SE=SD/\sqrt{20}$).

First lactation production was recorded two years after each female was born, allowing 13 years of data to accumulate for daughters of known sires. There were 500 herds in total across the four countries, with 10 new daughters each year per herd that would produce a first lactation record, which is 5000 new daughters over 13 years, or 65000 total daughters of known sires with production data (Table 3).

The relative numbers of international and single-country sires were not affected by selection in the base generation, being equal for both unselected or selected base generation populations ($P>.05$). Increases in the degree of semen exchange, however, had the expected effect of increasing ($P<.01$) the relative numbers of international sires and progeny of international sires. Average numbers of progeny per sire decreased for all types of sires, with increasing levels of semen exchange, because there were more sires in every country for the same number of matings when more sires were used in a greater number of

countries. Daughters of single-country sires represented 80% of the total when semen exchange was low, but only 57% of the total when semen exchange was high. Average numbers of daughters per sire were large enough, for all simulations, to compute national sire genetic evaluations of reasonable accuracy on the scale of each country.

Table 3. Numbers of simulated sires and progeny per sire.

	Number of countries with progeny				
	1	2	3	4	Total
Selected base generation, low semen exchange					
Sires	1067.8 ± 1.3	23.6 ± 0.5	5.8 ± 0.6	8.2 ± 0.3	1105.6 ± 1.3
Average progeny	48.7 ± 0.1	254.2 ± 3.3	381.3 ± 11.0	571.6 ± 8.3	58.8 ± 0.1
Total progeny	52028 ± 101	6015 ± 166	2228 ± 255	4729 ± 205	65000 ± 0
Selected base generation, moderate semen exchange					
Sires	1024.6 ± 1.3	45.5 ± 0.7	11.6 ± 0.8	17.7 ± 0.5	1099.3 ± 1.1
Average progeny	41.2 ± 0.1	192.8 ± 2.7	353.2 ± 7.4	564.7 ± 8.3	59.1 ± 0.1
Total progeny	42235 ± 103	8737 ± 101	4066 ± 294	9962 ± 236	65000 ± 0
Selected base generation, high semen exchange					
Sires	1011.0 ± 1.4	40.3 ± 0.7	16.1 ± 0.8	26.9 ± 0.4	1094.3 ± 1.0
Average progeny	36.7 ± 0.1	189.0 ± 2.8	339.1 ± 6.8	555.9 ± 6.4	59.4 ± 0.1
Total progeny	37055 ± 108	7607 ± 155	5399 ± 209	14939 ± 257	65000 ± 0
Unselected base generation, moderate semen exchange					
Sires	1023.4 ± 1.3	46.6 ± 1.1	12.3 ± 0.9	17.2 ± 0.5	1099.5 ± 1.0
Average progeny	41.4 ± 0.1	193.7 ± 2.0	341.0 ± 8.6	549.3 ± 6.3	59.1 ± 0.1
Total progeny	42345 ± 97	9014 ± 198	4202 ± 323	9438 ± 247	65000 ± 0

3.5.2. Criteria for Comparisons of Strategies

3.5.2.1. Errors of Prediction

With each replicated data set, the square root of the mean squared error of prediction (ERP) was computed for the lactation traits and the index of each country, for various groups of bulls as;

$$ERP = \sqrt{\frac{1}{n} \sum_{i=1}^n (\hat{g}_i - g_i)^2},$$

where $\hat{g}_i$ was the EBV and g_i the true BV for the i^{th} of n bulls, for a given trait, country, simulation and replicate. The EBV for all strategies were expressed relative to the average EBV of all local bulls, by subtracting the mean difference between EBV and BV for all local bulls, from all EBV computed on the scale of each country. Groups of bulls studied were;

- i. Local: bulls born in the country matching the country of evaluation.
- ii. Foreign: bulls born in other countries, and with no progeny in the country matching the country of evaluation.
- iii. Imported: bulls born in other countries, but with progeny recorded in the country matching the country of evaluation.
- iv. All: bulls born in all countries.
- v. Top: bulls from all countries with the highest predicted selection criterion for the country of interest.

The ERP for all groups except local bulls included a mean squared bias term for the difference between the mean EBV of the bull group relative to all local bulls, which is particularly relevant for international genetic comparisons, considering the importance of unbiased country comparisons discussed below. Local bulls were chosen as the unbiased reference group since they represented the largest bull group of interest on the scale of any country and were expected to be the least affected when changing international genetic evaluation strategies. The objective was to identify strategies with the smallest ERP, since smaller ERP would indicate more accurate predictions of true breeding value differences between animals, within the local populations and relative to animals from other countries.

3.5.2.2. Fairness of Country Comparisons

Fairness of country comparisons was assessed in terms of; i) bias on the local scale, and ii) bias on foreign scales. In each case, bulls born in the country of interest were compared against the corresponding groups of bulls from all other countries. These biases will often be referred to as country biases, since they reflect biased comparisons of the genetic means of bulls from different countries. Bias for bull group i relative to bull group k for any given trait, country, simulation and replicate was defined as;

$$\text{BIAS}_i = (\bar{\hat{g}}_i - \bar{\hat{g}}_k) - (\bar{g}_i - \bar{g}_k),$$

For bias on the local scale for bulls from EXP1, $\bar{\hat{g}}_i$ and $\bar{\hat{g}}_k$ were average evaluations on the scale of EXP1 for all EXP1 bulls and all bulls from the other three countries, respectively.

For bias on foreign scales, bias relative to local bulls was computed separately for each of the three foreign scales, then averaged. For example, for bulls from EXP1 on scale EXP2, $\bar{g}_i$ and $\bar{g}_k$ were average evaluations for bulls from EXP1 and EXP2 respectively, and on scale IMP1 were average evaluations for bulls from EXP1 and IMP1. The bias on foreign scales was the average bias across the three foreign scales.

Genetic improvement programs can be expensive to establish and operate, but any gains made in one generation of selection are perpetuated and cumulative for subsequent generations. Thus the benefits of genetic improvement can be substantial for progressive breeders. The availability of international genetic evaluations of sires facilitates increased trade of semen among countries and creates large revenue opportunities for countries with genetically superior sires. A desirable property of an international evaluation system is the fair treatment of all countries, such that country comparisons are unbiased, particularly because of the economic implications for breeders in one country over another. The objective was to identify strategies with the smallest biases.

3.5.2.3. Efficiency of Predicting Genetic Superiority

The efficiency with which a genetic evaluation strategy predicted genetic superiority was determined by computing the true genetic merits of the top bulls identified by the strategy. The average true genetic merit for the selection objective in each country was computed for the top 10 bulls that were identified using the corresponding selection criterion generated by the genetic evaluation strategy. Efficiency of predicting superiority is a key factor affecting the rates of genetic improvement that are feasible with a given genetic evaluation strategy.

3.5.3. Hypothesis Testing

The simulation design made it possible to generate t-statistics (parameter estimate / SE) for all parameters of interest (e.g. ERP). The t-statistics were easily computed without the use of a statistical software package (e.g. SAS) and were adequate to compare evaluation strategies within each simulation. An alternative approach that could have been used was to estimate the effects of evaluation strategies on the observed parameters of interest with a linear model. With the linear model approach, the effects of evaluation strategy could have been estimated within or across simulations, and interaction effects between evaluation strategy and levels of semen exchange or selection in base populations could have been tested for significance. The t-tests implicitly assumed these interactions were important, and despite having less power, were expected to yield similar results as a linear model approach that fitted evaluation strategies by simulation.

For the t-tests, all that was needed to assess significance was a set of thresholds to compare the t-statistics against. For all parameters being tested for significance, there were 20 replicates hence 19 degrees of freedom for each t-test. Thresholds for a t-test with 19 degrees of freedom can be taken from any standard t-table, as shown for a single test in Table 4. The single-test thresholds will be used for most inferences in the present study since specific comparisons of interest were envisaged prior to computing the statistics. In some cases, however, more conservative thresholds will be used in light of potential problems with multiple comparisons (Snedecor and Cochran, 1980).

Adjustments were made to the standard thresholds for the more conservative tests, to account for the higher probability of finding significant t-values by chance when multiple comparisons are made. Thresholds for 'n' independent tests were determined by

computing the probability of at least one significant result ($\alpha^*=1-(1-\alpha)^n$), and solving for the value of α that yielded the desired value for α^* ($\alpha=1-e^{(\ln(1-\alpha^*))/n}$). Thresholds were then taken from the standard t-table for the α -value corresponding with α^* , using linear interpolation when necessary.

A large number of strategies were studied and statistical parameters were estimated for multiple countries and different categories of bulls. Many of the results would be highly correlated, however, due to similarities among models, country population structures and genetic relationships among animals. The effective number of independent tests was too difficult to determine in many cases, but was generally assumed to range between 1 and 5, and was likely never more than 10 in the present study.

Inferences about statistical significance would be affected by the assumptions made in hypothesis testing regarding the number of independent tests. Hypothesis tests were limited as much as possible to comparisons of each alternative strategy against the theoretically best strategy, GAM, to minimize the effective number of independent tests. General patterns observed among the strategies were also considered, however, and will be discussed.

Table 4. Thresholds for two-tailed t-tests with 19 degrees of freedom.

Number of Independent tests	Level of Significance for 1 or more tests		
	.01	.05	.10
1	2.86	2.09	1.73
5	3.71	2.86	2.67
10	3.88	3.17	2.86

3.6. Results and Discussion

3.6.1. Simulated Data

3.6.1.1. Levels of Semen Exchange

Approximately 10%, 20% or 30% of cows in any given year were bred to bulls from foreign countries, for low, moderate and high levels of semen exchange, respectively (Table 5). The levels of semen exchange that exist in practice were compared with the simulated levels of exchange, by examining national sire evaluation files provided to Interbull for the May 1999 MACE run. Six countries that were major data contributors were identified and put into groups of four, regarding two as exporting and two as importing countries in correspondence with the four countries of the simulation. The levels of semen exchange that exist in practice (Tables 6 to 8) were assessed by comparing the relative proportions of local to foreign sires against the corresponding proportions from the simulation (Table 5).

The U.S.A. and Canada were regarded as exporting countries and France and Italy as importing countries in Table 6. The bulls born in the U.S.A. or Canada, in each of three consecutive decades, sired cows in all four countries, whereas the bulls born in France or Italy only sired cows in their respective home countries. The Netherlands and Germany were importing countries relative to the U.S.A. and Canada (Table 7), but were exporting countries relative to France and Italy (Table 8). For all three groups of countries, a combination of low, moderate and high levels of semen exchange was observed. The ranges in proportions of cows mated to local sires for these three groups of countries was much wider than between the simulations with low relative to high levels of semen exchange.

Therefore, results for all levels of semen exchange that were simulated, and extrapolations beyond the range of levels simulated, would have practical relevance for international evaluation of dairy sires.

Table 5. Proportions of cows sired by bulls from each country, in data simulated with selected base generations and three different levels of semen exchange among countries².

Cow country of birth	Sire country of birth			
	EXP1	EXP2	IMP1	IMP2
Low levels of semen exchange				
EXP1	0.904 ± 0.001	0.096 ± 0.001	0.000 ± 0.000	0.000 ± 0.000
EXP2	0.099 ± 0.001	0.901 ± 0.001	0.000 ± 0.000	0.000 ± 0.000
IMP1	0.064 ± 0.005	0.032 ± 0.005	0.904 ± 0.001	0.000 ± 0.000
IMP2	0.062 ± 0.006	0.034 ± 0.006	0.000 ± 0.000	0.904 ± 0.000
Moderate levels of semen exchange				
EXP1	0.814 ± 0.002	0.186 ± 0.002	0.000 ± 0.000	0.000 ± 0.000
EXP2	0.193 ± 0.001	0.807 ± 0.001	0.000 ± 0.000	0.000 ± 0.000
IMP1	0.108 ± 0.002	0.080 ± 0.003	0.812 ± 0.001	0.000 ± 0.000
IMP2	0.106 ± 0.002	0.080 ± 0.002	0.000 ± 0.000	0.814 ± 0.001
High levels of semen exchange				
EXP1	0.766 ± 0.004	0.234 ± 0.004	0.000 ± 0.000	0.000 ± 0.000
EXP2	0.279 ± 0.001	0.721 ± 0.001	0.000 ± 0.000	0.000 ± 0.000
IMP1	0.179 ± 0.004	0.095 ± 0.005	0.726 ± 0.001	0.000 ± 0.000
IMP2	0.171 ± 0.005	0.101 ± 0.006	0.000 ± 0.000	0.728 ± 0.001

²Mean ± SE over 20 replicates.

Table 6. Proportions of daughter records for protein yield, by sire country of first registration, for country group 1².

Cow country of record	Sire birth years	Sire country of first registration			
		U.S.A.	Canada	France	Italy
U.S.A	65-74	0.99 (L)	0.01 (L)	0.00	0.00
	75-84	0.98 (L)	0.02 (L)	0.00	0.00
	85-94	0.97 (L)	0.03 (L)	0.00	0.00
Canada	65-74	0.55 (H)	0.45 (H)	0.00	0.00
	75-84	0.48 (H)	0.52 (H)	0.00	0.00
	85-94	0.33 (H)	0.67 (H)	0.00	0.00
France	65-74	0.43 (H)	0.09 (M)	0.48 (H)	0.00
	75-84	0.73 (H)	0.08 (M)	0.19 (H)	0.00
	85-94	0.09 (M)	0.13 (H)	0.78 (H)	0.00
Italy	65-74	0.49 (H)	0.36 (H)	0.00	0.15 (H)
	75-84	0.51 (H)	0.25 (H)	0.00	0.24 (H)
	85-94	0.21 (H)	0.08 (M)	0.00	0.71 (H)

²L,M or H in parentheses indicates that the proportion suggests low, moderate or high levels of semen exchange, for comparison to the simulation results.

Table 7. Proportions of daughter records for protein yield, by sire country of first registration, for country group 2².

Cow country of record	Sire birth years	Sire country of first registration			
		U.S.A.	Canada	Netherlands	Germany
U.S.A	65-74	0.99 (L)	0.01 (L)	0.00	0.00
	75-84	0.98 (L)	0.02 (L)	0.00	0.00
	85-94	0.97 (L)	0.03 (L)	0.00	0.00
Canada	65-74	0.55 (H)	0.45 (H)	0.00	0.00
	75-84	0.48 (H)	0.52 (H)	0.00	0.00
	85-94	0.33 (H)	0.67 (H)	0.00	0.00
Netherlands	65-74	0.17 (H)	0.03 (L)	0.78 (H)	0.02 (L)
	75-84	0.37 (H)	0.05 (L)	0.48 (H)	0.11 (M)
	85-94	0.04 (L)	0.04 (L)	0.85 (M)	0.07 (L)
Germany	65-74	0.71 (H)	0.07 (L)	0.06 (L)	0.16 (H)
	75-84	0.27 (H)	0.17 (H)	0.01 (L)	0.55 (H)
	85-94	0.09 (M)	0.06 (L)	0.02 (L)	0.82 (M)

²L,M or H in parentheses indicates that the proportion suggests low, moderate or high levels of semen exchange, for comparison to the simulation results.

Table 8. Proportions of daughter records for protein yield, by sire country of first registration, for country group 3².

Cow country of record	Sire birth years	Sire country of first registration			
		Netherlands	Germany	France	Italy
Netherlands	65-74	0.98 (L)	0.01 (L)	0.00	0.00
	75-84	0.81 (M)	0.19 (M)	0.00	0.00
	85-94	0.91 (L)	0.09 (L)	0.00	0.00
Germany	65-74	0.26 (H)	0.74 (H)	0.00	0.00
	75-84	0.02 (L)	0.98 (L)	0.00	0.00
	85-94	0.03 (L)	0.96 (L)	0.01 (L)	0.00
France	65-74	0.14 (H)	0.03 (L)	0.83 (M)	0.00
	75-84	0.04 (L)	0.01 (L)	0.94 (L)	0.01 (L)
	85-94	0.04 (L)	0.00	0.95 (L)	0.01 (L)
Italy	65-74	0.00	0.00	0.00	0.99 (L)
	75-84	0.01 (L)	0.03 (L)	0.00	0.96 (L)
	85-94	0.03 (L)	0.01 (L)	0.01 (L)	0.95 (L)

²L, M or H in parentheses indicates that the proportion suggests low, moderate or high levels of semen exchange, for comparison to the simulation results.

Similarities of breeding objectives among the countries had only a minor effect on the relative amounts of semen exports. For example, with moderate semen exchange among countries, bulls from EXP1 were mated to 10.8% of the cows in IMP1 compared with 10.6% in IMP2 (Table 5). Mating proportions for EXP1 were only slightly higher in IMP1 than IMP2 for all levels of semen exchange, and for EXP2 were slightly higher or the same in IMP2 relative to IMP1. Although the index weights were very different for EXP1 and IMP1 relative to EXP2 and IMP2, the correlations among breeding objectives were quite similar among all pairs of countries (Table 9), due to the high genetic correlations among lactations within and across countries.

EXP1 sires had higher proportions of foreign country matings relative to EXP2 in both importing countries, even though the selection objective for IMP2 was closer to that of EXP2 (Table 5). Similarly, EXP1 had higher proportions of the matings in EXP2 than did EXP2 in EXP1, further demonstrating the advantage of the larger population size of EXP1. The effects of population size on the relative amounts of semen exports were much stronger than the effects of similarities of breeding objectives.

Table 9. Covariances (on and above diagonals) and correlations (below diagonals) among the breeding objectives of each country.

Country	EXP1	EXP2	IMP1	IMP2
EXP1	0.886	0.757	0.800	0.758
EXP2	0.864	0.867	0.750	0.770
IMP1	0.884	0.838	0.925	0.750
IMP2	0.861	0.885	0.834	0.874

3.6.1.2. Genetic Trends and Inbreeding

Base population (year 0) genetic means for cows in each country matched ($P>.10$) the simulation values of 0 for all countries with unselected base populations, and 0 and -1 for exporting and importing countries respectively, with selected base populations (Table 10). Genetic trends were initially much lower in all countries if base populations were unselected. By year 7, for example, exporting country cow populations had substantially lower genetic means and importing country cow populations had lost about 75% of their original genetic advantage with unselected relative to selected base populations. Reasons for this will be discussed below.

After year 7, differences in genetic gain were more similar between the simulations with selected or unselected base populations. The genetic means, which are unit-less, can be interpreted relative to the genetic variances of the merit indexes, which ranged from 0.867 for EXP2 to 0.925 for IMP1 (Table 9).

The relative trends for exporting countries can be seen more clearly, with the example of EXP2 in Figure 2. After year 7, rates of genetic change were essentially the same with unselected relative to selected base populations, and virtually unaffected by the levels of semen exchange. In importing countries, IMP2 for example (Figure 2), rates of genetic change after year 7 were higher when base generations were selected, due to the genetic advantage present in the exporting country populations. Rates of genetic change increased in the importing countries with higher levels of semen exchange, as expected with greater importation from the superior exporting country populations.

Base generation bull populations included proven bulls, shelved bulls and young bulls to be sample mated in the first year. Higher genetic trends in the cow populations

when base populations were selected are explained by the corresponding differences in genetic means for young bulls (Table 11), for example, which were not fully reflected in the cow populations until after year 7.

Inbreeding was kept to reasonably low levels in all countries but was not completely avoided (Table 12). The smaller exporting population accumulated the highest levels of inbreeding, as expected.

Table 10. True genetic means ($\pm$ SE) for overall merit of cows.

		Country ²			
Base generation	Semen exchange	EXP1	EXP2	IMP1	IMP2
Birth Year 0					
Selected	Low	0.000 ± 0.003	-0.005 ± 0.004	-1.005 ± 0.004	-0.998 ± 0.005
Selected	Moderate	0.000 ± 0.003	-0.005 ± 0.004	-1.005 ± 0.004	-0.998 ± 0.005
Selected	High	0.000 ± 0.003	-0.005 ± 0.004	-1.005 ± 0.004	-0.998 ± 0.005
Unselected	Moderate	0.000 ± 0.003	-0.004 ± 0.004	-0.012 ± 0.004	-0.003 ± 0.003
Birth Year 7					
Selected	Low	1.325 ± 0.026	1.308 ± 0.021	0.432 ± 0.027	0.381 ± 0.029
Selected	Moderate	1.336 ± 0.024	1.346 ± 0.023	0.513 ± 0.029	0.472 ± 0.026
Selected	High	1.349 ± 0.025	1.357 ± 0.024	0.603 ± 0.030	0.554 ± 0.026
Unselected	Moderate	0.775 ± 0.018	0.769 ± 0.024	0.784 ± 0.035	0.739 ± 0.026
Birth Year 15					
Selected	Low	2.840 ± 0.043	2.820 ± 0.042	2.158 ± 0.050	2.038 ± 0.061
Selected	Moderate	2.837 ± 0.039	2.883 ± 0.049	2.300 ± 0.054	2.213 ± 0.060
Selected	High	2.869 ± 0.038	2.877 ± 0.039	2.473 ± 0.051	2.353 ± 0.056
Unselected	Moderate	2.272 ± 0.031	2.201 ± 0.030	2.350 ± 0.057	2.186 ± 0.053

²EXP and IMP refer to exporting and importing, respectively.

Figure 2. Genetic means by year for overall merit of cows born in exporting country EXP2 and importing country IMP2, for simulations with unselected base populations and moderate levels of semen exchange, and with selected base populations and each of low, moderate and high levels of semen exchange.

Table 11. True genetic means ($\pm$ SE) for overall merit of bull calves selected for AI sample matings.

Base generation	Semen exchange	Country			
		EXP1	EXP2	IMP1	IMP2
Birth Year 0					
Selected	Low	1.052 ± 0.049	0.881 ± 0.074	-0.021 ± 0.057	-0.020 ± 0.060
Selected	Moderate	1.052 ± 0.049	0.881 ± 0.074	-0.021 ± 0.057	-0.020 ± 0.060
Selected	High	1.052 ± 0.049	0.881 ± 0.074	-0.021 ± 0.057	-0.020 ± 0.060
Unselected	Moderate	0.033 ± 0.052	0.030 ± 0.058	0.040 ± 0.071	0.024 ± 0.094
Birth Year 7					
Selected	Low	2.597 ± 0.050	2.521 ± 0.059	1.830 ± 0.085	1.739 ± 0.088
Selected	Moderate	2.570 ± 0.052	2.589 ± 0.051	1.862 ± 0.093	1.815 ± 0.077
Selected	High	2.626 ± 0.054	2.525 ± 0.065	1.979 ± 0.085	1.867 ± 0.069
Unselected	Moderate	1.941 ± 0.042	1.946 ± 0.072	2.056 ± 0.104	1.932 ± 0.082
Birth Year 15					
Selected	Low	4.050 ± 0.061	3.863 ± 0.070	3.379 ± 0.076	3.288 ± 0.097
Selected	Moderate	4.032 ± 0.064	4.081 ± 0.090	3.569 ± 0.102	3.325 ± 0.097
Selected	High	3.972 ± 0.058	4.037 ± 0.076	3.692 ± 0.078	3.634 ± 0.093
Unselected	Moderate	3.539 ± 0.071	3.396 ± 0.072	3.615 ± 0.096	3.250 ± 0.071

Table 12. Average inbreeding coefficient ($\pm$ SE) for females born in year 15.

Base generation	Semen exchange	Country			
		EXP1	EXP2	IMP1	IMP2
Selected	Low	0.032 $\pm$ 0.003	0.049 $\pm$ 0.004	0.040 $\pm$ 0.002	0.042 $\pm$ 0.003
Selected	Moderate	0.029 $\pm$ 0.002	0.045 $\pm$ 0.003	0.036 $\pm$ 0.003	0.039 $\pm$ 0.003
Selected	High	0.033 $\pm$ 0.003	0.044 $\pm$ 0.004	0.036 $\pm$ 0.002	0.042 $\pm$ 0.004
Unselected	Moderate	0.027 $\pm$ 0.002	0.034 $\pm$ 0.002	0.032 $\pm$ 0.002	0.033 $\pm$ 0.002

3.6.1.3. Weighting Factors for the MACE Strategies

Three different sets of weighting factors were used in the alternative MACE strategies, which were described in Table 1. The number of daughters (ND) was the simplest weighting factor and the first to be used by Interbull, from 1994 to 2000. The weighting factor described by Interbull (2000), referred to as effective daughter contributions (Ne) is used currently by Interbull to apply MACE with a single trait and multiple countries. The weighting factor described in Appendix 2 is referred to as effective independent daughter records (Ni) and is proposed for use in MACE with multiple traits and multiple countries.

Means and linear relationships among the alternative weighting factors were similar for all simulations, and are shown for one simulation in Table 13. Sequential culling resulted in fewer daughter records, and hence lower means for ND, Ne and Ni in later lactations. Factors Ne and Ni were less consistent in the patterns of decrease for different bulls, and decreased less than ND with later lactations (Figure 3). Factor Ne tended to increase from first to second lactation, then decrease in the third lactation for bulls with relatively fewer daughters, while Ni increased from second to third lactation for bulls with only 20 daughters. The decrease going from first to third lactation was always highest for ND and lowest for Ne, with Ni intermediate as expected.

The minimum ND for first lactation was 20, by design of the simulation, and for lactations 2 and 3 the minimum ND was 0. Regression estimates for Ne would be greater than ND for almost all observed values of ND. For example, the regression estimates for Ne were greater than ND for all values of ND higher than 24, -7 and -8 for first, second and third lactation respectively (Table 13). The regression estimates for Ni were generally

greater than ND for lactation 3 only, since bulls with 2 or more daughter records in lactation 3 had N_i greater than ND. For lactation 2, N_i were less than ND for bulls with fewer than 27 daughter records, and for lactation 1, N_i were less than ND for bulls with fewer than 321 daughter records.

Factor N_e could theoretically have been lower than ND because N_e was adjusted downwards, relative to ND, due to information loss in the estimation of management group effects in NAM. However, this decrease in N_e was offset by an increase due to correlated trait information, especially for the later lactations where ND was smaller. Factor N_i was always smaller than N_e , for all lactations, because of the positive genetic correlations between the lactation traits (see Appendix 2 for derivation of N_i relative to N_e).

Table 13. Means and linear relationships among the alternative weighting factors used in the MACE analyses, based on the simulated data with selected base populations and moderate levels of semen exchange.

Trait	Mean weighting factor ^z for bulls with daughter records (ND ₁ >0)					
	ND	Ne	Ni			
Lactation 1	53.2 ± 0.05	53.9 ± 0.05	50.1 ± 0.05			
Lactation 2	37.0 ± 0.04	51.5 ± 0.05	39.7 ± 0.06			
Lactation 3	26.2 ± 0.03	46.4 ± 0.05	38.8 ± 0.05			
Index	53.2 ± 0.05	44.9 ± 0.04				
Estimates from linear regression ^y on ND						
	Dependent variable Ne			Dependent variable Ni		
	Intercept	Slope	Ne=ND ^w	Intercept	Slope	Ni=ND
Lactation 1	-0.55	1.02	24	-3.75	1.01	321
Lactation 2	2.31	1.33	-7	-6.87	1.26	27
Lactation 3	4.86	1.59	-8	-1.10	1.52	2
Index	-1.09	0.86	-8			

^zNe are effective daughter contributions described by Interbull (2000), Ni are effective independent daughter lactation records described in Appendix 2.

^yData were pooled across countries and replicates to create, by trait, more than 20000 observations to estimate 2 parameters. All model R² values were greater than 0.95.

^wpoint on the regression line where Ne=ND

Figure 3. Average weighting factors, by lactation, for bulls with different numbers of daughters. Ne are effective daughter contributions (Interbull, 2000), Ni are effective independent daughter lactation records (Appendix 2), and ND are numbers of daughters.

3.6.2. Errors of Prediction

3.6.2.1. By Bull Category

The GAM consistently gave equal ($P>.10$) or smaller errors ($P<.01$) than all other strategies, for all categories of bulls, when base populations were unselected (Table 14). Advantages of GAM were generally smallest when compared with RSe or any of the MT strategies, and largest when compared with the CNV and NAM strategies.

Differences between MTr and the lowest-ERP strategies in the CNV or NAM classes, as proportions of the corresponding difference for GAM were 0.88 for foreign and all bulls and 0.99 for imported bulls. The RSe and all MT strategies were equivalent to GAM ($P>.10$) for ERP of top bulls. The ERP for local bulls were the least affected by the choice of evaluation strategies, all differences among strategies being less than 1%. Although GAM had significantly lower ERP ($P<.01$) for local bulls than all other strategies, the differences were small.

Advantages of GAM were smaller when base populations were selected, for all bull categories except local bulls. The RSe and MT strategies had lower ERP than GAM for predicting genetic merit of top bulls ($P<.05$) when base populations were selected. Top bulls are the most important group for international evaluations, since they are the primary candidates for use in international breeding programs.

Table 14. Differences in ERP^z, and ERP for GAM, for overall merit across evaluation scales of all countries, for different groups of bulls, with moderate levels of semen exchange among countries (t-value in parentheses).

Strategies ^y	Bulls included				
	Local	Foreign	Imported	All	Top ^w
Unselected base populations					
CNV1-GAM	0.003 (5.1)	0.040 (11.9)	0.235 (29.3)	0.036 (13.4)	0.036 (4.2)
STn-GAM	0.002 (4.2)	0.021 (10.0)	0.018 (5.1)	0.017 (10.2)	0.002 (0.3)
STe-GAM	0.002 (4.3)	0.020 (10.2)	0.014 (4.4)	0.016 (10.3)	0.000 (0.0)
CNV2-GAM	0.003 (5.1)	0.024 (9.0)	0.204 (25.2)	0.023 (10.9)	0.032 (5.0)
NAM-GAM	0.003 (5.1)		0.088 (14.0)		
RSn-GAM	0.003 (5.0)	0.001 (0.8)	0.025 (5.1)	0.002 (1.8)	0.008 (2.4)
RSe-GAM	0.002 (4.3)	0.003 (2.0)	0.003 (1.0)	0.003 (2.4)	0.002 (0.5)
MTr-GAM	0.002 (4.0)	0.003 (2.4)	0.001 (0.5)	0.003 (2.7)	-0.002 (-0.4)
MTn-GAM	0.002 (4.1)	0.004 (3.0)	0.006 (2.2)	0.004 (3.3)	0.002 (0.5)
MTe-GAM	0.002 (4.3)	0.006 (3.6)	0.020 (4.8)	0.006 (4.0)	0.005 (1.0)
MTi-GAM	0.002 (4.3)	0.006 (3.3)	0.014 (3.8)	0.005 (3.8)	0.002 (0.4)
GAM	0.466 ± 0.002	0.615 ± 0.003	0.289 ± 0.004	0.574 ± 0.003	0.579 ± 0.010
Selected base populations					
CNV1-GAM	0.003 (4.2)	0.022 (6.3)	0.226 (32.1)	0.022 (7.7)	0.026 (3.0)
STn-GAM	0.002 (3.9)	0.017 (5.4)	0.012 (4.7)	0.014 (5.5)	-0.003 (-0.5)
STe-GAM	0.003 (4.3)	0.016 (5.3)	0.011 (4.7)	0.013 (5.4)	-0.004 (-0.7)
CNV2-GAM	0.003 (4.2)	0.002 (0.6)	0.207 (30.4)	0.006 (2.4)	0.017 (2.4)
NAM-GAM	0.003 (4.2)		0.067 (13.6)		
RSn-GAM	0.004 (6.1)	-0.009 (-3.6)	0.035 (5.2)	-0.006 (-2.9)	-0.002 (-0.5)
RSe-GAM	0.003 (4.3)	-0.006 (-2.2)	0.003 (1.5)	-0.004 (-1.9)	-0.011 (-2.7)
MTr-GAM	0.002 (3.9)	-0.005 (-1.6)	-0.004 (-2.6)	-0.003 (-1.4)	-0.013 (-3.1)
MTn-GAM	0.002 (3.5)	-0.004 (-1.4)	0.000 (0.0)	-0.003 (-1.2)	-0.012 (-2.7)
MTe-GAM	0.002 (3.6)	-0.002 (-0.6)	0.012 (3.5)	-0.001 (-0.4)	-0.009 (-1.9)
MTi-GAM	0.002 (3.8)	-0.003 (-0.9)	0.007 (2.3)	-0.002 (-0.7)	-0.010 (-2.1)
GAM	0.463 ± 0.002	0.659 ± 0.005	0.299 ± 0.005	0.608 ± 0.004	0.591 ± 0.010

^zERP included prediction error variance and prediction bias relative to all local bulls.

^wtop 10 evaluated bulls from each country.

^yStrategies are described in Table 1.

The ERP for all strategies were highest for foreign bulls, because this group did not have local daughters. The ERP for foreign bulls were consistently smaller for strategies that included three lactation traits per country relative to strategies that included only one index trait per country, and MACE relative to conversion strategies, whether or not base populations were selected. The strategy proposed by VanRaden et al. (2000), described in section 2.3 but not considered for the present study, would theoretically be intermediate between CNV and MACE strategies, for both ERP and ease of application.

Strategies ranked similarly for ERP of imported bulls relative to foreign bulls, but the advantages of MACE over CNV strategies were much larger for the imported bulls. The CNV strategies relied solely on each bull's national EBV from his country of birth, whereas the MACE strategies used national EBV from all countries where a bull was proven. By contrast, NAM used the bull's proof in each country of interest (i.e. second country EBV for imported bulls and first country EBV for local bulls). While NAM had lower ERP than conversions for imported bulls, it had higher ERP than all of the MACE strategies, whether or not base populations were selected.

The most common strategies in practice for dairy cattle are NAM for local and imported bulls, and STe for foreign bulls. Genetic merit of both foreign and imported bulls could be predicted with lower ERP by using RSe, any of the MT strategies or GAM.

The ERP of local and imported bulls with GAM were essentially unaffected by the levels of semen exchange (Figure 4). Foreign, top and all bulls were evaluated with lower ERP, however, as semen exchange increased. The ERP for all bulls were intermediate between local and foreign bulls for all levels of semen exchange.

The ERP trends for the MACE strategies were similar to those depicted for GAM in Figure 4. The relative magnitudes of the effects of semen exchange, on the ERP of all bulls, for selected strategies from each class can be seen in Figure 5. The GAM was the most sensitive to the levels of semen exchange, followed by the MACE strategies which were all similarly affected, and the conversion strategies were the least affected. The relative sensitivities of the strategies were also apparent in Table 15, where ERP differences for all strategies relative to GAM, were more positive for all groups of bulls with higher levels of semen exchange.

The above results, in summary, suggest that the GAM strategy should be preferred to minimize ERP for the entire population of bulls if base populations are unselected or if semen exchange is high, but not if base populations are selected and levels of semen exchange are low. The MT strategies gave ERP for all bulls that were almost as low or sometimes lower than GAM, considering all simulations, and should be preferred over GAM to minimize ERP for top bulls. The MT strategies are also simpler computationally than GAM, requiring substantially less computer memory and time.

The choice of weighting factors for the MACE strategies had only minor, but consistent effects on ERP with unselected or selected base populations (Table 14) and for different levels of semen exchange (Table 15). The bulls most affected were the imported bulls. The use of Ne instead of ND reduced ERP of imported bulls for both the ST and RS strategies (STe and RSe instead of STn and RSn), as expected following Fikse and Banos (2001). The reductions in ERP were much smaller for the ST than for the RS strategies, likely because of smaller differences between Ne and ND for the index trait than for the lactation traits (Table 13).

Figure 4. ERP for different groups of bulls, with the global animal model (GAM) strategy and selected base populations.

Figure 5. ERP for all bulls, with selected base populations and alternative levels of semen exchange among countries.

Table 15. Differences in ERP, and ERP for GAM, for overall merit across evaluation scales of all countries, for different groups of bulls, with selected base populations and low or high levels of semen exchange (t-value in parentheses).

Strategies	Bulls included				
	Local	Foreign	Imported	All	Top ^w
Low levels of semen exchange					
CNV1-GAM	0.002 (4.3)	-0.001 (-0.1)	0.218 (21.3)	0.002 (0.3)	0.014 (2.2)
STn-GAM	0.002 (4.4)	0.007 (1.4)	0.007 (2.7)	0.006 (1.5)	-0.003 (-0.5)
STe-GAM	0.002 (4.6)	0.006 (1.3)	0.004 (1.7)	0.005 (1.4)	-0.005 (-0.8)
CNV2-GAM	0.002 (4.3)	-0.021 (-3.7)	0.194 (20.8)	-0.015 (-3.2)	0.003 (0.4)
NAM-GAM	0.002 (4.3)		0.073 (14.9)		
RSn-GAM	0.003 (5.7)	-0.022 (-6.0)	0.037 (3.2)	-0.017 (-5.6)	-0.009 (-1.6)
RSe-GAM	0.002 (4.6)	-0.019 (-4.9)	-0.004 (-1.6)	-0.015 (-4.7)	-0.016 (-4.8)
MTr-GAM	0.002 (4.2)	-0.018 (-4.4)	-0.009 (-3.6)	-0.014 (-4.2)	-0.022 (-6.7)
MTn-GAM	0.002 (4.0)	-0.020 (-4.6)	-0.005 (-1.5)	-0.016 (-4.4)	-0.023 (-6.3)
MTe-GAM	0.002 (4.2)	-0.017 (-4.1)	0.009 (2.5)	-0.013 (-3.9)	-0.020 (-5.8)
MTi-GAM	0.002 (4.1)	-0.018 (-4.2)	0.002 (0.6)	-0.014 (-4.0)	-0.022 (-5.8)
GAM	0.455 ± 0.002	0.698 ± 0.007	0.286 ± 0.008	0.642 ± 0.006	0.626 ± 0.017
High levels of semen exchange					
CNV1-GAM	0.005 (10.6)	0.038 (14.9)	0.245 (36.0)	0.036 (17.4)	0.055 (5.5)
STn-GAM	0.004 (9.2)	0.021 (8.8)	0.021 (10.2)	0.017 (9.2)	0.011 (1.6)
STe-GAM	0.005 (9.2)	0.020 (8.8)	0.018 (10.6)	0.017 (9.2)	0.009 (1.4)
CNV2-GAM	0.005 (10.6)	0.015 (6.8)	0.221 (40.7)	0.017 (10.1)	0.045 (6.5)
NAM-GAM	0.005 (10.6)		0.079 (20.7)		
RSn-GAM	0.006 (9.7)	-0.004 (-1.8)	0.031 (5.7)	-0.001 (-0.7)	0.015 (2.8)
RSe-GAM	0.005 (9.0)	-0.002 (-0.7)	0.007 (5.8)	-0.000 (-0.1)	0.002 (0.4)
MTr-GAM	0.004 (8.7)	0.000 (0.1)	0.003 (1.8)	0.001 (0.6)	0.000 (0.0)
MTn-GAM	0.004 (8.9)	0.001 (0.3)	0.008 (4.2)	0.002 (0.8)	0.001 (0.3)
MTe-GAM	0.005 (9.2)	0.002 (0.8)	0.021 (8.8)	0.003 (1.4)	0.007 (1.4)
MTi-GAM	0.005 (9.1)	0.002 (0.7)	0.015 (7.3)	0.003 (1.2)	0.005 (1.0)
GAM	0.466 ± 0.003	0.643 ± 0.005	0.290 ± 0.005	0.594 ± 0.004	0.550 ± 0.013

^wtop 10 evaluated bulls from each country

The ranking of MT strategies, from lowest to highest ERP for imported bulls, was MTr, MTn, MTi, MTe. The MTi strategy was theoretically expected to have lower ERP than MTn because the Ni weighting factors accounted for more information than ND. However, the differences between MTi and MTn were small. The ERP for MTi would likely be relatively smaller in practice due to greater variability in data structures and NAM strategies among countries than were simulated in the present study (Emanuelson et al., 1999). The MTi strategy takes better account of this variability than either MTn or MTr (Fikse and Banos, 2001). The MTi strategy had the best theoretical foundation among the MT strategies that used weighting factors instead of weighting blocks, and was a good simplified alternative to the MTr strategy of Schaeffer (2001), which used weighting blocks.

Strategies MTi and GAM are compared in more detail in Figure 6, for the simulations with selected base populations. Prediction errors were generally higher for local and imported bulls with MTi, while for foreign and top bulls MTi had lower prediction errors than GAM. Therefore, GAM had lower ERP than MACE when bulls had local proofs, but not when predicting performance in countries where the bulls did not have a local proof.

Figure 6. Differences in ERP for different groups of bulls, for a multiple-trait MACE model relative to GAM (MTi - GAM), with selected base populations.

3.6.2.2 By Country

Prediction errors for GAM in exporting countries were higher in the smaller EXP2 relative to the larger EXP1, and were also higher in EXP2 than either of the importing countries, for unselected and selected base populations (Table 16) and low and high levels of semen exchange (Table 17). The lower ERP for EXP1 are explained by the higher proportion of local to foreign bulls in EXP1, since local bulls generally had much lower ERP than foreign bulls (Figure 4). Prediction errors were smaller in importing countries because three countries were represented in the sires-of-cows populations in importing countries compared with only two for the exporting countries.

The ERP with strategies from the RS and MT classes were higher than with GAM ($P < .01$) for EXP1, but similar for the other three countries ($P > .10$), when base populations were unselected (Table 16). With selected base populations, all RS and MT strategies had lower ERP than GAM for EXP2 ($P < .05$) and similar ERP for the other three countries ($P > .10$). The ERP for EXP2 were highest relative to the other countries for all strategies, with either unselected or selected base populations. The ERP for EXP1 were relatively higher, when compared with IMP1 and IMP2, if base populations were selected rather than unselected.

The MT strategies gave lower ERP than GAM for all countries when semen exchange was low, but differences were not significant ($P > .10$) for IMP1 or IMP2 (Table 17). The significant differences for EXP2 ($P < .01$) were approximately twice as large as the significant differences ($P < .05$) for EXP1, probably because the ERP was much larger for GAM in EXP2 relative to EXP1.

Table 16. Differences in ERP, and ERP for GAM, for overall merit of all bulls, by country of evaluation, with moderate levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of evaluation			
	EXP1	EXP2	IMP1	IMP2
Unselected base populations				
CNV1-GAM	0.038 (9.9)	0.023 (8.5)	0.047 (11.9)	0.036 (6.6)
STn-GAM	0.016 (5.8)	0.013 (3.7)	0.024 (8.0)	0.013 (6.4)
STe-GAM	0.015 (5.6)	0.012 (3.6)	0.024 (8.1)	0.013 (6.6)
CNV2-GAM	0.029 (9.7)	0.019 (8.5)	0.022 (6.8)	0.024 (5.9)
RSn-GAM	0.005 (3.0)	-0.002 (-0.6)	0.002 (1.2)	0.002 (1.6)
RSe-GAM	0.007 (3.8)	0.002 (0.8)	0.002 (1.1)	0.001 (1.3)
MTr-GAM	0.007 (3.6)	0.003 (0.9)	0.002 (0.9)	0.001 (0.7)
MTn-GAM	0.008 (3.6)	0.003 (1.0)	0.003 (1.3)	0.002 (1.3)
MTe-GAM	0.010 (4.0)	0.006 (1.7)	0.004 (1.8)	0.003 (1.9)
MTi-GAM	0.009 (3.9)	0.005 (1.5)	0.003 (1.6)	0.003 (1.6)
GAM	0.550 ± 0.004	0.594 ± 0.004	0.575 ± 0.005	0.576 ± 0.005
Selected base populations				
CNV1-GAM	0.009 (2.5)	0.001 (0.2)	0.039 (9.0)	0.039 (9.3)
STn-GAM	0.012 (3.0)	0.003 (0.6)	0.020 (10.0)	0.021 (7.1)
STe-GAM	0.010 (2.7)	0.003 (0.6)	0.020 (10.2)	0.021 (7.2)
CNV2-GAM	-0.001 (-0.5)	-0.008 (-2.0)	0.018 (5.4)	0.017 (5.3)
RSn-GAM	-0.005 (-1.4)	-0.020 (-5.2)	0.001 (0.9)	0.001 (0.7)
RSe-GAM	-0.002 (-0.7)	-0.016 (-3.8)	0.002 (1.0)	0.001 (0.5)
MTr-GAM	0.001 (0.3)	-0.015 (-3.4)	0.002 (1.1)	0.000 (0.1)
MTn-GAM	0.001 (0.4)	-0.015 (-3.2)	0.002 (1.3)	0.001 (0.3)
MTe-GAM	0.003 (1.0)	-0.012 (-2.3)	0.003 (1.7)	0.002 (1.0)
MTi-GAM	0.002 (0.8)	-0.012 (-2.5)	0.003 (1.5)	0.002 (0.8)
GAM	0.602 ± 0.007	0.659 ± 0.009	0.579 ± 0.003	0.588 ± 0.004

Table 17. Differences in ERP, and ERP for GAM, for overall merit of all bulls, by country of evaluation, with selected base populations and low or high levels of semen exchange (t-value in parentheses).

Strategies	Country of evaluation			
	EXP1	EXP2	IMP1	IMP2
Low levels of semen exchange				
CNV1-GAM	-0.011 (-1.1)	-0.045 (-5.3)	0.031 (3.9)	0.036 (4.7)
STn-GAM	0.001 (0.2)	-0.009 (-1.2)	0.016 (4.8)	0.017 (4.5)
STe-GAM	0.000 (0.0)	-0.008 (-1.1)	0.015 (4.8)	0.016 (4.3)
CNV2-GAM	-0.023 (-2.9)	-0.052 (-7.6)	0.008 (1.1)	0.011 (2.0)
RSn-GAM	-0.020 (-4.7)	-0.034 (-5.7)	-0.005 (-1.9)	-0.007 (-2.6)
RSe-GAM	-0.017 (-3.9)	-0.031 (-5.2)	-0.004 (-1.7)	-0.005 (-1.8)
MTr-GAM	-0.014 (-3.0)	-0.031 (-5.1)	-0.004 (-1.6)	-0.006 (-2.1)
MTn-GAM	-0.015 (-3.1)	-0.032 (-5.1)	-0.005 (-1.8)	-0.007 (-2.2)
MTe-GAM	-0.013 (-2.7)	-0.030 (-4.6)	-0.004 (-1.4)	-0.004 (-1.6)
MTi-GAM	-0.014 (-2.8)	-0.030 (-4.7)	-0.004 (-1.5)	-0.005 (-1.6)
GAM	0.643 ± 0.009	0.708 ± 0.011	0.607 ± 0.006	0.601 ± 0.006
High levels of semen exchange				
CNV1-GAM	0.033 (8.9)	0.010 (2.7)	0.054 (18.5)	0.049 (11.5)
STn-GAM	0.016 (4.5)	0.009 (1.9)	0.025 (11.9)	0.020 (8.5)
STe-GAM	0.014 (4.1)	0.010 (2.1)	0.024 (11.9)	0.020 (9.1)
CNV2-GAM	0.020 (6.8)	-0.001 (-0.2)	0.026 (9.5)	0.026 (9.7)
RSn-GAM	-0.001 (-0.5)	-0.008 (-2.2)	0.003 (1.7)	0.003 (2.1)
RSe-GAM	0.001 (0.3)	-0.006 (-1.5)	0.003 (1.5)	0.003 (1.4)
MTr-GAM	0.004 (1.3)	-0.004 (-0.9)	0.002 (1.4)	0.003 (1.2)
MTn-GAM	0.005 (1.3)	-0.003 (-0.8)	0.003 (1.7)	0.003 (1.5)
MTe-GAM	0.006 (1.7)	-0.002 (-0.3)	0.004 (2.0)	0.005 (2.1)
MTi-GAM	0.005 (1.5)	-0.002 (-0.4)	0.003 (1.9)	0.004 (1.9)
GAM	0.588 ± 0.007	0.628 ± 0.008	0.579 ± 0.004	0.577 ± 0.004

3.6.3. Fairness of Country Comparisons

3.6.3.1. Bias on the Local Scale

When base populations were unselected, local bulls were disadvantaged, relative to all foreign bulls, by the biases observed for GAM ($P < .05$) on the scales of all countries (Table 18). The largest disadvantages were for the exporting countries, and in particular EXP2. Similar patterns of bias were observed for most of the other genetic evaluation strategies, with differences in bias between EXP1 and EXP2 generally smaller and between IMP1 and IMP2 generally larger than they were with GAM. The GAM had larger biases than most alternative strategies for EXP2 ($P < .05$), IMP1 ($P > .10$) and IMP2 ($P < .01$), and smaller bias for EXP1 ($P < .05$).

Local bulls were disadvantaged in the exporting countries ($P < .01$), but not in the importing countries ($P > .10$), when base populations were selected (Table 18). The biases in the exporting countries were much larger with selected than with unselected base populations. With selected base populations, biases were always larger for GAM than the other strategies ($P < .01$). Differences in bias between EXP1 and EXP2 were again larger for GAM than the other strategies, as was the case with unselected base populations.

Biases in exporting countries were reduced, for all strategies, by increasing the levels of semen exchange (Table 19). The reductions in bias were largest for GAM, consistent with the greater sensitivity of GAM to the levels of semen exchange that was observed for ERP in the previous section (Table 17). The ERP were strongly affected by

the biased comparisons of local relative to foreign bulls in each country, because those biases were part of the ERP as discussed in section 3.5.2.1.

Differences in bias, for all strategies relative to GAM, were smaller but in the same direction on the scales of exporting countries, with higher levels of semen exchange. In contrast, the corresponding ERP were lower with low levels of semen exchange, and higher with high levels of semen exchange (Table 17). The GAM would have been the strategy with the lowest ERP for all levels of semen exchange if not for the country biases. For example, the within-country ERP (ERP_w), computed by subtracting the effects of the country biases, for GAM and MTi with low levels of semen exchange, were respectively 0.513 and 0.537 for EXP1, and 0.573 and 0.597 for EXP2, computing ERP_w as follows;

$$ERP_w = \sqrt{ERP^2 - BIAS^2}$$

For example, taking ERP from Table 17 and BIAS from Table 19, for GAM in country EXP1 with low levels of semen exchange:

$$\begin{aligned} ERP_w &= \sqrt{0.643^2 - (-0.387)^2} \\ &= 0.513 \end{aligned}$$

Evaluations of local bulls relative to foreign bulls in the importing countries were unbiased ($P > .10$), when base populations were selected and levels of semen exchange were moderate (Table 18) or high (Table 19). The local bulls in importing countries had

bias advantages over foreign bulls when semen exchange was low ($P < .05$), with GAM and all MACE strategies that evaluated multiple traits in each country (the RS and MT strategies). The biases favouring local bulls in the importing countries, when semen exchange was low, were much smaller but corresponded with the advantages observed for those same bulls on the scales of the exporting countries (i.e. the disadvantages for local bulls in EXP1 and EXP2).

The magnitudes of the biases in exporting countries, when semen exchange was low, were approximately 50-80% of the simulated true differences in genetic means of the base generation populations of the countries being compared. For example, the EXP1 biases were -0.33 for the RS and MT strategies (Table 19), while the difference in genetic means for the base generation population of EXP1 relative to the average for the other three countries was 0.67. For EXP2, biases with GAM were -0.42 and the corresponding difference in genetic means for the base generation was 0.50. All of the genetic evaluation strategies were able to account very well for the simulated differences in base generation country means on importing country scales of evaluation, but only a portion of the differences on the evaluation scales of exporting countries. The strategies did a better job of accounting for base generation differences with higher levels of semen exchange, but even with high levels of semen exchange, biases on the scales of exporting countries were equal to approximately one third of the corresponding true differences in the base generation.

Table 18. Bias on the local scale, for overall merit of all bulls, with moderate levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of birth			
	EXP1	EXP2	IMP1	IMP2
Unselected base populations				
CNV1	-0.190 (-9.3)	-0.140 (-7.4)	-0.020 (-0.8)	0.080 (3.2)
STn	-0.170 (-12.5)	-0.138 (-6.5)	-0.091 (-4.0)	-0.016 (-0.7)
STe	-0.166 (-12.1)	-0.140 (-6.7)	-0.091 (-4.0)	-0.023 (-1.0)
CNV2	-0.183 (-8.5)	-0.184 (-10.1)	0.037 (1.7)	0.040 (1.5)
RSn	-0.150 (-9.4)	-0.139 (-7.6)	-0.060 (-2.7)	-0.048 (-2.2)
RSe	-0.157 (-10.3)	-0.145 (-7.2)	-0.054 (-2.5)	-0.019 (-0.3)
MTr	-0.155 (-10.0)	-0.146 (-7.5)	-0.053 (-2.5)	-0.025 (-1.1)
MTn	-0.156 (-10.0)	-0.144 (-7.2)	-0.054 (-2.5)	-0.026 (-1.2)
MTe	-0.160 (-10.3)	-0.143 (-6.8)	-0.051 (-2.3)	-0.015 (-0.7)
MTi	-0.158 (-10.2)	-0.144 (-6.9)	-0.052 (-2.4)	-0.017 (-0.8)
GAM	-0.137 (-7.7)	-0.171 (-9.9)	-0.068 (-3.1)	-0.061 (-2.7)
CNV2 - GAM	-0.046 (-5.5)	-0.013 (-1.7)	0.105 (11.1)	0.101 (7.2)
STe - GAM	-0.029 (-2.9)	0.031 (2.7)	-0.023 (-2.5)	0.038 (3.5)
RSe - GAM	-0.020 (-2.5)	0.025 (2.3)	0.014 (1.7)	0.042 (5.4)
MTi - GAM	-0.022 (-2.4)	0.027 (2.4)	0.016 (1.6)	0.044 (4.6)
MTr - GAM	-0.018 (-2.2)	0.025 (2.6)	0.015 (1.7)	0.036 (4.5)
Selected base populations				
CNV1	-0.265 (-14.3)	-0.280 (-13.0)	-0.021 (-1.0)	0.000 (0.0)
STn	-0.292 (-14.3)	-0.272 (-12.0)	-0.013 (-0.6)	-0.019 (-0.7)
STe	-0.289 (-14.4)	-0.277 (-12.4)	-0.011 (-0.5)	-0.026 (-1.0)
CNV2	-0.257 (-13.0)	-0.301 (-14.2)	0.022 (1.0)	0.003 (0.1)
RSn	-0.266 (-13.1)	-0.261 (-12.3)	0.011 (0.5)	-0.012 (-0.5)
RSe	-0.270 (-13.0)	-0.263 (-12.3)	0.016 (0.8)	0.007 (0.3)
MTr	-0.275 (-13.1)	-0.263 (-12.5)	0.021 (1.0)	0.010 (0.5)
MTn	-0.273 (-12.9)	-0.259 (-12.1)	0.018 (0.9)	0.007 (0.3)
MTe	-0.272 (-12.6)	-0.260 (-11.8)	0.022 (1.0)	0.010 (0.4)
MTi	-0.272 (-12.7)	-0.261 (-12.0)	0.021 (1.0)	0.009 (0.4)
GAM	-0.296 (-17.2)	-0.329 (-16.8)	0.006 (0.3)	-0.013 (-0.6)
CNV2 - GAM	0.038 (5.5)	0.028 (2.7)	0.016 (1.3)	0.016 (1.1)
STe - GAM	0.007 (0.8)	0.052 (4.1)	-0.017 (-2.0)	-0.012 (-0.9)
RSe - GAM	0.026 (3.3)	0.066 (6.3)	0.010 (1.4)	0.020 (2.1)
MTi - GAM	0.024 (3.0)	0.068 (5.8)	0.015 (1.6)	0.023 (2.2)
MTr - GAM	0.021 (2.7)	0.066 (6.6)	0.015 (1.7)	0.024 (2.4)

Table 19. Bias on the local scale, for overall merit of all bulls, with selected base populations and low or high levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of birth			
	EXP1	EXP2	IMP1	IMP2
Low levels of semen exchange				
CNV1	-0.322 (-13.1)	-0.295 (-12.1)	0.030 (0.9)	0.040 (1.1)
STn	-0.360 (-19.3)	-0.346 (-13.6)	0.036 (1.2)	0.042 (1.5)
STe	-0.358 (-19.4)	-0.352 (-14.0)	0.038 (1.3)	0.036 (1.3)
CNV2	-0.306 (-12.7)	-0.323 (-12.5)	0.089 (2.5)	0.035 (1.2)
RSn	-0.326 (-16.4)	-0.333 (-12.2)	0.067 (2.2)	0.047 (2.0)
RSe	-0.330 (-16.3)	-0.332 (-12.7)	0.070 (2.3)	0.068 (2.8)
MTr	-0.333 (-16.8)	-0.328 (-13.0)	0.075 (2.5)	0.069 (3.1)
MTn	-0.331 (-17.0)	-0.322 (-12.5)	0.068 (2.3)	0.064 (2.9)
MTe	-0.332 (-16.4)	-0.320 (-11.9)	0.071 (2.4)	0.071 (3.1)
MTi	-0.331 (-16.4)	-0.322 (-12.2)	0.070 (2.4)	0.071 (3.1)
GAM	-0.387 (-23.7)	-0.416 (-17.9)	0.096 (3.4)	0.073 (3.0)
CNV2 - GAM	0.080 (4.9)	0.093 (7.6)	-0.007 (-0.3)	-0.038 (-1.9)
STe - GAM	0.028 (3.0)	0.064 (4.4)	-0.058 (-4.4)	-0.036 (-2.2)
RSe - GAM	0.057 (5.8)	0.084 (6.1)	-0.026 (-2.0)	-0.005 (-0.4)
MTi - GAM	0.055 (5.2)	0.094 (6.5)	-0.026 (-1.7)	-0.002 (-0.1)
MTr - GAM	0.053 (5.1)	0.088 (6.7)	-0.021 (-1.4)	-0.003 (-0.2)
High levels of semen exchange				
CNV1	-0.288 (-14.2)	-0.193 (-10.9)	-0.051 (-2.1)	0.037 (1.8)
STn	-0.254 (-14.3)	-0.216 (-13.8)	-0.049 (-2.3)	-0.004 (-0.2)
STe	-0.250 (-14.2)	-0.222 (-14.2)	-0.047 (-2.2)	-0.012 (-0.7)
CNV2	-0.276 (-13.8)	-0.223 (-12.0)	0.009 (0.4)	0.023 (1.1)
RSn	-0.223 (-12.8)	-0.218 (-13.1)	-0.018 (-0.8)	-0.010 (-0.5)
RSe	-0.229 (-13.0)	-0.216 (-13.5)	-0.013 (-0.6)	0.010 (0.5)
MTr	-0.234 (-13.1)	-0.217 (-13.8)	-0.009 (-0.4)	0.016 (0.8)
MTn	-0.233 (-12.9)	-0.213 (-13.4)	-0.009 (-0.4)	0.012 (0.7)
MTe	-0.233 (-12.6)	-0.211 (-13.2)	-0.006 (-0.3)	0.016 (0.8)
MTi	-0.231 (-12.6)	-0.213 (-13.4)	-0.008 (-0.4)	0.016 (0.8)
GAM	-0.255 (-15.5)	-0.261 (-14.5)	-0.042 (-1.8)	-0.023 (-1.1)
CNV2 - GAM	-0.021 (-2.1)	0.038 (3.6)	0.051 (5.1)	0.046 (4.7)
STe - GAM	0.005 (0.7)	0.038 (4.3)	-0.005 (-0.6)	0.011 (1.2)
RSe - GAM	0.026 (3.3)	0.044 (5.8)	0.029 (4.5)	0.033 (4.3)
MTi - GAM	0.023 (2.9)	0.047 (5.6)	0.035 (4.4)	0.039 (4.0)
MTr - GAM	0.021 (2.6)	0.044 (5.9)	0.034 (5.0)	0.039 (4.4)

3.6.3.2. Bias on Foreign Scales

Biases on foreign scales of evaluation, for all genetic evaluation strategies, created large advantages ($P < .01$) for bulls born in the importing countries when base populations were unselected or selected (Table 20) and with low or high levels of semen exchange (Table 21). The biases were larger with selected base populations, lower levels of semen exchange, and with GAM relative to other strategies, consistent with the bias results previously discussed that disadvantaged bulls born in exporting countries on their local scales of evaluation.

The bulls from exporting countries were evaluated without bias on foreign scales ($P > .05$), for both EXP1 and EXP2, with all strategies when base populations were unselected, without bias ($P > .10$) for EXP1 and with negative bias ($P < .01$) for EXP2 when base populations were selected (Table 20). The biases on foreign scales were presumably smaller for bulls born in exporting than importing countries, because exporting country bulls had progeny with performance data in foreign countries.

Biases for all strategies and all countries decreased with increasing levels of semen exchange (Table 21), the largest decreases being observed for GAM, consistent with the corresponding results for bias on local scales and for ERP, previously discussed. The increasing levels of semen exchange would have increased genetic connectedness and hence accuracies of predicted genetic differences between the countries.

Observed biases on both local and foreign scales showed that none of the strategies could predict country differences without bias on the scales of exporting countries, whether or not base populations were selected, particularly for importing relative to exporting country bulls. An explanation may be that performance data sets in the exporting countries

were not directly connected to the importing country populations, since bulls from importing countries were not used in the exporting countries. There was no genetic representation for the importing country populations in the performance data recorded by the exporting countries. The importing countries, in contrast, had progeny of sires from both of the exporting countries that could be used by each genetic evaluation strategy to predict genetic differences among countries on the scales of importing countries. Hence, country biases were consistently smaller on the scales of importing countries than they were on the scales of exporting countries.

The GAM may provide unbiased estimates of country differences on the scale of a given country, for all countries that have sufficient genetic representation in the performance data of the country of interest, but not necessarily for countries without or with minimal genetic representation. Predictions for bulls from these latter countries, relative to local bulls, may have less bias if derived using MACE or CNV strategies, particularly if base populations are selected.

Table 20. Bias on foreign country scales, for overall merit of all bulls, with moderate levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of birth			
	EXP1	EXP2	IMP1	IMP2
Unselected base populations				
CNV1	-0.049 (-2.2)	-0.018 (-0.8)	0.146 (6.6)	0.266 (9.9)
STn	0.030 (1.7)	-0.002 (-0.1)	.0185 (10.8)	0.253 (11.7)
STe	0.035 (2.0)	0.001 (0.1)	.0187 (11.1)	0.247 (11.8)
CNV2	-0.031 (-1.3)	-0.051 (-2.4)	0.209 (9.7)	0.230 (8.2)
RSn	0.043 (2.3)	-0.003 (-0.2)	0.182 (11.2)	0.214 (9.8)
RSe	0.023 (1.3)	-0.021 (-1.2)	0.194 (11.4)	0.228 (10.0)
MTr	0.028 (1.5)	-0.019 (-1.1)	0.195 (11.9)	0.222 (9.7)
MTn	0.028 (1.5)	-0.016 (-0.9)	0.195 (11.6)	0.222 (9.3)
MTe	0.018 (1.0)	-0.023 (-1.3)	0.198 (10.9)	0.227 (9.0)
MTi	0.021 (1.1)	-0.021 (-1.2)	0.196 (11.1)	0.226 (9.2)
GAM	0.076 (4.0)	0.004 (0.3)	0.181 (11.8)	0.200 (9.8)
CNV2 - GAM	-0.106 (-8.5)	-0.056 (-5.0)	0.028 (2.3)	0.030 (2.4)
STe - GAM	-0.041 (-4.5)	-0.003 (-0.5)	0.006 (0.4)	0.048 (3.4)
RSe - GAM	-0.052 (-6.8)	-0.025 (-4.4)	0.013 (1.2)	0.028 (2.9)
MTi - GAM	-0.055 (-6.0)	-0.026 (-3.8)	0.015 (1.2)	0.026 (2.4)
MTr - GAM	-0.048 (-5.6)	-0.024 (-4.0)	0.014 (1.2)	0.023 (2.5)
Selected base populations				
CNV1	0.005 (0.3)	-0.007 (-0.3)	0.332 (10.5)	0.330 (11.9)
STn	-0.016 (-0.9)	-0.034 (-2.3)	0.392 (15.0)	0.370 (14.5)
STe	-0.010 (-0.6)	-0.034 (-2.3)	0.395 (15.1)	0.365 (14.3)
CNV2	0.012 (0.6)	-0.028 (-1.5)	0.326 (12.0)	0.303 (9.9)
RSn	-0.009 (-0.5)	-0.041 (-2.7)	0.340 (14.2)	0.335 (12.6)
RSe	-0.026 (-1.4)	-0.054 (-3.7)	0.352 (14.5)	0.344 (13.0)
MTr	-0.032 (-1.7)	-0.054 (-3.7)	0.355 (15.1)	0.346 (13.5)
MTn	-0.031 (-1.7)	-0.050 (-3.3)	0.352 (14.9)	0.343 (13.2)
MTe	-0.036 (-1.9)	-0.055 (-3.5)	0.358 (14.8)	0.345 (13.0)
MTi	-0.034 (-1.8)	-0.055 (-3.6)	0.357 (14.9)	0.344 (13.0)
GAM	0.015 (1.0)	-0.045 (-3.1)	0.391 (15.3)	0.367 (14.0)
CNV2 - GAM	-0.003 (-0.2)	0.016 (1.5)	-0.065 (-6.4)	-0.064 (-4.1)
STe - GAM	-0.025 (-2.8)	0.011 (1.5)	0.004 (0.3)	-0.002 (-0.1)
RSe - GAM	-0.041 (-5.6)	-0.010 (-1.8)	-0.039 (-4.0)	-0.023 (-2.1)
MTi - GAM	-0.049 (-5.6)	-0.010 (-1.6)	-0.034 (-3.0)	-0.023 (-2.0)
MTr - GAM	-0.047 (-5.8)	-0.009 (-1.7)	-0.036 (-3.5)	-0.021 (-1.9)

Table 21. Bias on foreign country scales, for overall merit of all bulls, with selected base populations and low or high levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of birth			
	EXP1	EXP2	IMP1	IMP2
Low levels of semen exchange				
CNV1	-0.047 (-1.5)	-0.023 (-0.8)	0.375 (11.3)	0.364 (9.7)
STn	-0.048 (-1.9)	-0.111 (-5.1)	0.470 (16.2)	0.453 (14.2)
STe	-0.042 (-1.7)	-0.111 (-5.1)	0.472 (16.4)	0.449 (14.1)
CNV2	-0.036 (-1.2)	-0.052 (-2.0)	0.379 (11.7)	0.316 (8.3)
RSn	-0.041 (-1.7)	-0.121 (-5.5)	0.414 (15.0)	0.407 (13.1)
RSe	-0.059 (-2.5)	-0.135 (-6.3)	0.423 (15.2)	0.416 (13.3)
MTr	-0.062 (-2.6)	-0.138 (-6.6)	0.426 (15.8)	0.414 (13.6)
MTn	-0.059 (-2.5)	-0.132 (-6.4)	0.421 (15.6)	0.413 (13.8)
MTe	-0.067 (-2.7)	-0.138 (-6.7)	0.424 (15.3)	0.415 (13.8)
MTi	-0.065 (-2.6)	-0.138 (-6.6)	0.424 (15.3)	0.415 (13.7)
GAM	-0.046 (-2.6)	-0.138 (-6.9)	0.490 (18.2)	0.456 (13.6)
CNV2 - GAM	0.010 (0.4)	0.086 (5.1)	-0.111 (-6.5)	-0.140 (-7.2)
STe - GAM	0.004 (0.3)	0.027 (3.1)	-0.018 (-0.9)	-0.007 (-0.4)
RSe - GAM	-0.012 (-1.1)	0.004 (0.5)	-0.067 (-5.6)	-0.040 (-3.0)
MTi - GAM	-0.019 (-1.5)	0.001 (0.1)	-0.067 (-4.6)	-0.041 (-2.8)
MTr - GAM	-0.016 (-1.3)	0.001 (0.1)	-0.065 (-4.7)	-0.042 (-2.9)
High levels of semen exchange				
CNV1	-0.041 (-1.8)	0.056 (3.2)	0.258 (8.9)	0.331 (13.0)
STn	-0.011 (-0.6)	-0.018 (-1.1)	0.314 (15.4)	0.339 (15.0)
STe	-0.003 (-0.2)	-0.018 (-1.1)	0.318 (15.6)	0.332 (14.5)
CNV2	-0.026 (-1.2)	0.027 (1.8)	0.270 (10.3)	0.287 (11.7)
RSn	0.004 (0.2)	-0.029 (-1.8)	0.276 (13.3)	0.296 (12.1)
RSe	-0.013 (-0.7)	-0.041 (-2.6)	0.285 (13.8)	0.304 (12.6)
MTr	-0.020 (-1.1)	-0.042 (-2.7)	0.290 (14.1)	0.306 (13.2)
MTn	-0.019 (-1.0)	-0.038 (-2.5)	0.288 (13.9)	0.301 (13.1)
MTe	-0.024 (-1.3)	-0.041 (-2.6)	0.291 (14.1)	0.301 (13.2)
MTi	-0.022 (-1.2)	-0.042 (-2.6)	0.289 (14.0)	0.301 (13.0)
GAM	0.029 (1.6)	-0.006 (-0.4)	0.313 (13.1)	0.326 (12.5)
CNV2 - GAM	-0.055 (-4.2)	0.033 (2.6)	-0.043 (-5.1)	-0.039 (-4.2)
STe - GAM	-0.032 (-4.3)	-0.012 (-2.0)	0.005 (0.6)	0.006 (0.6)
RSe - GAM	-0.042 (-6.2)	-0.034 (-7.2)	-0.028 (-3.5)	-0.022 (-2.4)
MTi - GAM	-0.050 (-6.7)	-0.036 (-6.3)	-0.024 (-2.4)	-0.025 (-2.2)
MTr - GAM	-0.048 (-6.7)	-0.036 (-7.6)	-0.023 (-2.7)	-0.021 (-2.0)

3.6.4. Efficiency of Predicting Genetic Superiority

The average true genetic merits of top bulls, when averaged across the scales of all countries (Column All of Table 22), were generally not different ($P>.05$) between GAM and any of the MACE strategies, but were significantly lower ($P<.01$) for both CNV strategies, with unselected or selected base populations. Genetic merits of top bulls were also similar ($P>.05$) for the MACE strategies relative to GAM, with low or high levels of semen exchange (Table 23). Relative to GAM, genetic merits of top bulls for CNV2 were similar ($P>.10$) when semen exchange was high, but lower ($P<.01$) when semen exchange was low, and for CNV1 were lower ($P<.01$) with both low and high levels of semen exchange. Hence, CNV1 was a less efficient strategy for predicting genetic superiority.

There were no notable differences among countries in relative efficiencies of the strategies for predicting genetic superiority. Countries EXP1 and IMP1, however, had higher genetic means for the true top bulls, than did EXP2 and IMP2 in all simulations, likely because of differences in the selection criteria used by each country. Countries EXP1 and IMP1 placed 90-100% emphasis on only two of the three lactation traits in their selection criteria, compared with relatively equal emphasis on all three lactation traits for EXP2 and IMP2. Variances of the selection criteria were therefore higher for EXP1 and IMP1 (Table 9). The larger population size of EXP1 may have also been an important factor (Banos and Smith, 1991).

Table 22. Differences in true overall merit for top^z 10 evaluated bulls from each country, by country of evaluation, with moderate levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of evaluation				
	EXP1	EXP2	IMP1	IMP2	All ^w
Unselected base populations					
CNV1-GAM	-0.017 (-1.8)	-0.021 (-1.4)	-0.044 (-2.6)	-0.047 (-3.6)	-0.032 (-3.5)
STn-GAM	-0.004 (-0.5)	-0.004 (-0.5)	-0.027 (-2.0)	-0.019 (-1.6)	-0.014 (-2.4)
STe-GAM	-0.004 (-0.5)	-0.004 (-0.4)	-0.025 (-1.9)	-0.013 (-1.2)	-0.012 (-2.0)
CNV2-GAM	-0.010 (-1.0)	-0.017 (-1.5)	-0.020 (-1.9)	-0.032 (-3.5)	-0.020 (-3.3)
RSn-GAM	-0.010 (-1.5)	0.001 (0.1)	-0.006 (-1.3)	-0.001 (-0.1)	-0.004 (-1.0)
RSe-GAM	-0.005 (-0.8)	0.002 (0.4)	-0.007 (-1.3)	0.003 (0.3)	-0.002 (-0.4)
MTr-GAM	-0.006 (-1.2)	0.003 (0.7)	-0.010 (-2.0)	-0.003 (-0.4)	-0.004 (-1.4)
MTn-GAM	-0.013 (-2.3)	0.001 (0.2)	-0.011 (-2.6)	-0.006 (-0.7)	-0.007 (-2.1)
MTe-GAM	-0.005 (-0.9)	0.000 (0.0)	-0.014 (-2.4)	0.000 (0.0)	-0.005 (-1.0)
MTi-GAM	-0.006 (-1.3)	0.002 (0.4)	-0.014 (-2.3)	0.003 (0.3)	-0.004 (-0.8)
GAM	3.289 ± 0.042	3.163 ± 0.047	3.364 ± 0.049	3.180 ± 0.047	3.249 ± 0.041
TRUE	3.667 ± 0.035	3.580 ± 0.035	3.721 ± 0.042	3.560 ± 0.042	3.632 ± 0.034
GAM / TRUE	0.897	0.884	0.904	0.893	0.895
Selected base populations					
CNV1-GAM	-0.032 (-2.9)	-0.033 (-3.2)	-0.058 (-4.4)	-0.032 (-2.5)	-0.039 (-5.6)
STn-GAM	-0.001 (-0.1)	0.004 (0.6)	-0.024 (-2.4)	-0.015 (-1.5)	-0.009 (-1.9)
STe-GAM	-0.006 (-0.7)	0.011 (1.4)	-0.023 (-2.4)	-0.013 (-1.6)	-0.008 (-1.6)
CNV2-GAM	-0.024 (-2.5)	-0.017 (-1.6)	-0.036 (-3.8)	-0.010 (-0.9)	-0.022 (-3.3)
RSn-GAM	-0.008 (-0.9)	-0.011 (-1.2)	0.001 (0.2)	-0.007 (-0.7)	-0.006 (-1.1)
RSe-GAM	-0.005 (-0.8)	0.002 (0.3)	-0.003 (-0.4)	-0.009 (-1.1)	-0.004 (-0.8)
MTr-GAM	-0.008 (-1.5)	0.000 (0.0)	-0.005 (-0.6)	-0.004 (-0.5)	-0.004 (-1.0)
MTn-GAM	-0.007 (-1.3)	0.003 (0.4)	-0.007 (-0.8)	-0.001 (-0.2)	-0.003 (-0.8)
MTe-GAM	-0.010 (-1.8)	0.007 (0.8)	-0.002 (-0.2)	-0.005 (-0.7)	-0.003 (-0.7)
MTi-GAM	-0.008 (-1.4)	0.009 (1.3)	-0.001 (-0.1)	-0.004 (-0.6)	-0.001 (-0.2)
GAM	3.616 ± 0.062	3.530 ± 0.071	3.633 ± 0.065	3.485 ± 0.073	3.566 ± 0.061
TRUE	3.957 ± 0.060	3.909 ± 0.067	3.964 ± 0.067	3.895 ± 0.066	3.931 ± 0.059
GAM / TRUE	0.914	0.903	0.916	0.895	0.907

^zbulls with the highest values for the within-country selection criteria.

^waverage across the four country scales.

Table 23. Differences in true overall merit for top 10 evaluated bulls from each country, by country of evaluation, with selected base populations and low or high levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of evaluation				
	EXP1	EXP2	IMP1	IMP2	All
Low levels of semen exchange					
CNV1-GAM	-0.026 (-4.1)	-0.045 (-4.5)	-0.043 (-3.1)	-0.048 (-4.6)	-0.040 (-6.4)
STn-GAM	-0.003 (-0.4)	-0.014 (-1.4)	-0.006 (-0.5)	-0.014 (-1.9)	-0.009 (-2.0)
STe-GAM	0.000 (0.0)	-0.015 (-1.6)	-0.005 (-0.5)	-0.015 (-1.7)	-0.009 (-1.9)
CNV2-GAM	-0.016 (-1.6)	-0.030 (-3.5)	-0.023 (-2.0)	-0.026 (-2.8)	-0.024 (-4.2)
RSn-GAM	0.006 (0.7)	-0.016 (-2.6)	0.005 (0.6)	-0.011 (-1.6)	-0.004 (-1.0)
RSe-GAM	0.009 (1.7)	-0.002 (-0.2)	0.004 (0.6)	0.009 (2.3)	0.005 (1.4)
MTr-GAM	0.002 (0.2)	-0.001 (-0.1)	-0.004 (-0.5)	0.009 (2.2)	0.002 (0.4)
MTn-GAM	-0.002 (-0.3)	0.001 (0.2)	-0.001 (-0.1)	0.001 (0.2)	0.000 (0.0)
MTe-GAM	0.001 (0.1)	0.005 (0.9)	0.001 (0.1)	0.009 (1.7)	0.004 (0.9)
MTi-GAM	0.000 (0.0)	0.008 (1.3)	-0.003 (-0.3)	0.007 (1.5)	0.003 (0.8)
GAM	3.500 ± 0.043	3.415 ± 0.050	3.547 ± 0.055	3.387 ± 0.052	3.462 ± 0.043
TRUE	3.855 ± 0.040	3.774 ± 0.045	3.904 ± 0.053	3.782 ± 0.045	3.829 ± 0.039
GAM / TRUE	0.908	0.905	0.909	0.896	0.904
High levels of semen exchange					
CNV1-GAM	-0.024 (-2.9)	-0.036 (-3.3)	-0.055 (-3.9)	-0.042 (-2.7)	-0.039 (-4.1)
STn-GAM	-0.005 (-0.8)	-0.009 (-0.9)	-0.022 (-2.2)	-0.015 (-1.5)	-0.013 (-2.5)
STe-GAM	-0.008 (-1.0)	-0.007 (-0.7)	-0.019 (-1.9)	-0.017 (-1.6)	-0.013 (-2.4)
CNV2-GAM	-0.014 (-1.4)	-0.011 (-1.0)	-0.023 (-2.1)	-0.004 (-0.3)	-0.013 (-1.6)
RSn-GAM	-0.009 (-1.4)	-0.004 (-0.5)	-0.013 (-1.3)	-0.021 (-2.4)	-0.012 (-3.1)
RSe-GAM	-0.010 (-1.7)	0.004 (0.6)	-0.012 (-1.2)	-0.008 (-1.1)	-0.006 (-1.8)
MTr-GAM	-0.004 (-0.5)	0.007 (1.2)	-0.015 (-1.5)	-0.001 (-0.1)	-0.003 (-0.8)
MTn-GAM	-0.002 (-0.3)	0.006 (1.1)	-0.026 (-2.5)	-0.005 (-0.7)	-0.007 (-1.7)
MTe-GAM	-0.005 (-0.8)	-0.005 (-0.8)	-0.027 (-2.6)	-0.013 (-1.6)	-0.013 (-2.8)
MTi-GAM	-0.004 (-0.6)	-0.002 (-0.3)	-0.024 (-2.8)	-0.010 (-1.8)	-0.010 (-2.8)
GAM	3.728 ± 0.058	3.647 ± 0.056	3.754 ± 0.059	3.647 ± 0.060	3.694 ± 0.050
TRUE	4.053 ± 0.055	4.002 ± 0.052	4.083 ± 0.057	3.992 ± 0.055	4.032 ± 0.048
GAM / TRUE	0.920	0.911	0.919	0.914	0.916

The selection of top bulls using GAM was about 90% efficient for all simulations, based on the ratio of true genetic means for top bulls selected by GAM relative to the theoretical maximum (bulls selected based on true genetic merit). These ratios were always slightly higher for EXP1 and IMP1 relative to EXP2 and IMP2, suggesting that the accuracy of evaluation for top bulls may have been slightly higher for EXP1 and IMP1 relative to EXP2 and IMP2. The ratios were also higher with selected than with unselected base populations (Table 22) and with high versus low levels of semen exchange (Table 23), reflecting different accuracies of evaluation for top bulls among the simulations.

The practical importance of the observed differences among strategies for genetic merit of top bulls is probably very small. Consider for example that genetic trends for cows over the last eight years of the simulation with unselected base populations (derived from Table 10) ranged from 0.179 to 0.196 per year among the four countries. The largest observed difference in true merit of top bulls for the same simulation was 0.047 between CNV1 and GAM for IMP2 (Table 22), equivalent to only 3 months of genetic progress. The genetic progress made in each simulation was achieved with NAM strategies, but with structured initiatives by all countries to sample and progeny-test superior foreign-country bulls. Initiatives such as these may be more important than the accuracy of the international evaluations.

Proportions of bulls in common among strategies, when selecting the top 10 (about 1% of all) bulls for each country generally ranged from 0.75 to 0.95 with both unselected (Table 24) and selected base populations (Table 25). The corresponding proportions in common with the true top bulls ranged from approximately 0.35 to 0.40, being much lower because the true top bulls would include young bulls not yet progeny-tested. Most models,

regardless of differences that may have existed in ERP or bias, generally identified the same groups of bulls as being the best. The GAM, MTi and MTr approaches, for example, had 90-95% top selected bulls in common, and each had between 84% and 89% in common with the top bulls selected by STe.

The GAM had similar proportions of bulls in common with the true top bull lists, for any proportion selected, when compared against MACE strategies that allowed either one trait (STe) or multiple traits (MTi) per country (Figure 7). The conversion approaches, in contrast, had consistently lower proportions of bulls in common with the true top lists, for any proportion selected. Essentially the same advantages of using GAM instead of CNV strategies could therefore be more easily achieved by using STe or MTi.

Table 24. Proportions in common, averaged across scales of evaluation for all countries, for top 10 bulls on each scale, for alternative evaluation strategies with unselected base populations (proportion above and SE below the diagonal).

Strategy	TRUE ^z	GAM	MTr	MTi	STe	CNV2	CNV1
TRUE		0.391	0.387	0.389	0.384	0.352	0.349
GAM	0.019		0.929	0.910	0.840	0.827	0.774
MTr	0.019	0.007		0.951	0.861	0.804	0.753
MTi	0.018	0.008	0.009		0.863	0.812	0.758
STe	0.019	0.013	0.014	0.013		0.759	0.792
CNV2	0.023	0.013	0.016	0.018	0.018		0.856
CNV1	0.018	0.015	0.017	0.017	0.014	.009	

^zBulls selected based on true genetic merit. All other strategies are described in Table 1.

Table 25. Proportions in common, averaged across scales of evaluation for all countries, for top 10 bulls on each scale, for alternative evaluation strategies with selected base populations (proportion above and SE below the diagonal).

Strategy	TRUE ^z	GAM	MTr	MTi	STe	CNV2	CNV1
TRUE		0.408	0.393	0.400	0.391	0.369	0.361
GAM	0.019		0.926	0.896	0.861	0.802	0.765
MTr	0.019	0.011		0.939	0.887	0.794	0.763
MTi	0.019	0.010	0.006		0.891	0.788	0.764
STe	0.021	0.009	0.007	0.009		0.748	0.765
CNV2	0.019	0.014	0.017	0.014	0.015		0.877
CNV1	0.018	0.014	0.015	0.013	0.016	0.011	

^zBulls selected based on true genetic merit. All other strategies are described in Table 1.

Figure 7. Proportions of selected bulls in common with true top bulls, by proportion selected.

3.6.5. General Discussion

The GAM had the lowest ERP among all strategies, for all groups of bulls when base populations were unselected. When the assumption of no selection in base populations was violated, however, ERP for GAM were relatively higher compared with the MACE and CNV strategies, and multiple-trait MACE strategies had the lowest ERP for foreign and top bulls among all strategies. The GAM strategy had relatively higher ERP with selected base populations because of country biases that were relatively higher for GAM when base populations were selected.

Significant country biases were found for all strategies, giving unfair advantages to foreign bulls evaluated on the scales of exporting countries, when base populations were unselected or selected. Country biases were not unexpected when the assumption of no selection in the base generation was violated, and were larger with selected than with unselected base populations. However, no biases were expected with unselected base populations, particularly for GAM using all data and pedigree related to selection decisions that were made during the simulation.

These latter biases can be explained by the fact that bulls from importing countries were not used for breeding in the exporting countries. Since genetic correlations among countries were less than unity, the evaluations for those bulls on the scales of the exporting countries were predictions for correlated traits, with no data available for the correlated traits of interest. The predictions for those bulls would have been affected by the solutions for genetic groups from the importing countries, which were also correlated trait predictions because of the groups-random approach that was

used. If groups had been treated as fixed, however, the above group effects would have been non-estimable.

The predictions for all genetic group effects under the groups-random approach were based on an incorrect implied assumption that equivalent genetic samples were drawn from each genetic group in all countries. Alternative genetic group definitions could avoid this assumption, but may not be practical and were not considered in the present study. In reality, higher selection intensities were used to select proven foreign bulls than unproven young local bulls, violating the above assumption. The violation of this assumption caused a downward regression of the genetic group solutions for exporting countries on the scales of the importing countries. The downwards regression for genetic groups from the exporting countries made the genetic groups for local bulls look relatively better than they should have on the scales of the importing countries. There were progeny data in the importing countries for sires from both exporting and importing countries, however, that created compensating estimates of sire deviations from the genetic group effects. Country biases were reduced on the scales of the importing countries when the genetic group and sire deviation effects were combined in the EBV. Similar compensating sire deviations could not be estimated for sires from importing countries on the scales of the exporting countries, because there were no progeny data in the exporting countries for bulls from the importing countries. Hence the bias in country comparisons inherent in the group solutions showed up more prominently in the sire EBV on the scales of the exporting countries.

The country biases could possibly be decreased by assuming traits were genetically identical on the scales of all countries, avoiding the prediction of correlated trait evaluations

on the scales of exporting countries for bulls from importing countries. Further studies would be needed to test this hypothesis, preferably with simulation since true breeding values would be needed to compute the biases.

Powell and Norman (2000) compared MACE strategies that used either estimated genetic correlations, among eight countries, or assumed genetic correlations near unity for dairy production traits, the implied assumption of the latter strategy being that traits were genetically identical on all country scales. Their criteria for comparing strategies were indicators of the accuracy of international evaluations for predicting future national evaluations. The criteria they used may have been positively associated with ERP of the international evaluations, including both the country biases and the within-country ERP. They found no appreciable differences between strategies for the criteria they used. In a subsequent study, Powell et al. (2002) detected significant country effects on the international evaluations of full-brother families when estimated genetic correlations were used in MACE. The country effects were generally smaller when genetic correlations near unity were assumed. The country effects were referred to as country biases, although they may simply have been evidence that genotype-by-country effects were significant and that true genetic correlations among countries were not unity for the traits studied.

When genetic correlations are less than unity, genetic correlations of unity could be assumed for a portion of the genetic effects by partitioning genetic effects into the main effects and the interaction-by-country effects. Togashi et al. (1999) proposed such a strategy, ignoring genetic relationships among sires for the sire-by-country effects, but not for the main effects of sires across countries. This type of strategy would combine potential benefits of removing genetic groups-by-country interaction effects, as with the strategy

proposed by Powell and Norman (2000), while still allowing sires to re-rank across country scales. Removing the groups-by-country interaction effect has not yet been proven to reduce country biases, however, since this hypothesis was not tested.

Problems of bias were notably larger for GAM than for the MACE strategies when base populations were selected. The GAM performed relatively better as the levels of semen exchange increased, but continued to create the largest biases even at the highest levels of semen exchange. There may be unexpected advantages in using a MACE strategy instead of GAM, to limit potential problems of bias when comparing sires from different countries.

Larger country biases for GAM than the alternative strategies may have been due to differences between animal and sire-based strategies that affected genetic group solutions. With the sire-based MACE strategies, for example, the compensating estimates of deviations from genetic group effects were limited to sires, whereas with GAM there could also be compensating estimates for management group effects and mates of sires, allowing larger country biases to remain in the genetic group solutions.

There were very small differences in average true genetic merits of top bulls identified by each strategy. Only major strategy changes increased the average true genetic merits of top bulls, for example switching from conversions to any of the MACE strategies or GAM ($P < .05$), or using information on all traits within each country instead of limiting the information to one trait per country. These observations were the same whether or not base populations were selected. Differences in true genetic merits of top bulls were generally small because of very high proportions of bulls in common when selecting by the alternative strategies. There was greater than 90% bulls in common, for example, between

the top 1% of sires identified by GAM or MT strategies, with either unselected or selected base populations.

The effects of the weighting factors used in MACE strategies were relatively minor, for all criteria used to compare strategies. There were only small reductions in ERP, for example, if weighting factors for the ST and RS strategies were based on effective daughter information rather than numbers of daughters. The MACE strategies using the theoretically preferred weighting factors generally had smaller ERP, but not always for MT strategies. separate studies would be needed to assess the effects of alternative weighting factors for situations where data structures or NAM strategies are more variable among countries (Fikse and Banos, 2001). The STe, RSe and MTi strategies would be expected to have relatively lower ERP compared with alternative MACE strategies in each class, for those situations.

The MT class of strategies was very similar to RSe for all criteria studied, while the ST class of strategies had relatively higher ERP in many cases. The RS strategies are not useful when the number of traits of interest varies among countries, however, which would often be the case in practice. For those situations, the MT class of strategies can be used as demonstrated by Sullivan and Wilton (2001).

Among the MT strategies, MTr (proposed by Schaeffer, 2001) had the lowest ERP in general but with very small differences compared to MTn and MTi. The MTi strategy would be expected to have relatively lower ERP in practice, since MTi takes account of differences in NAM strategies that are very common among countries (Emanuelson et al., 1999), which MTr and MTn ignore. The MTi strategy is also easier to implement than MTr because MTi uses diagonalized weighting blocks (i.e. weighting factors instead of blocks)

for sires. The diagonalization of weighting blocks effectively allows traits within a country to be treated computationally as if they were separate countries, enabling software designed for the original MACE strategy (Schaeffer, 1994) to more easily accommodate multiple traits per country.

Genetic covariances would generally need to be estimated to apply any of the strategies from the current study to field data. Sensitivity of each strategy to errors in covariance component estimates was not a part of the present study, and may affect the results when applying the strategies with estimated variances and covariances. The general findings should apply, however, assuming similar difficulties would arise when estimating the similar sets of variances and covariances that are required for each of the strategies.

Errors in covariance estimation may be larger for the more complicated strategies, particularly if computational limits prevent the use of favoured approaches and it becomes necessary to use more approximate covariance estimation procedures. These limits should be temporary, however, as computer technology continues to advance. Strategy comparisons should not be altered based on temporary differences that may no longer exist when it comes time to implement any of the procedures considered in the present study.

The covariances used for the GAM were the correct parameters, but for the MACE strategies they were only approximations. The covariances used for MACE were taken from those used for GAM, without considering the effects that alternative weighting factors (Fikse and Banos, 1999b) and selection of bull dams (Bulmer, 1971) are known to have on genetic covariance component estimates. The ERP for MACE strategies might have been even smaller than was observed if better covariance components had been used. Alternatively, it may be unnecessary to re-estimate the

covariance components for MACE within each country, as proposed by Schaeffer (2001), since these parameters could be derived from the covariances used for NAM by each country.

The findings of the present study are most applicable to lactation-specific traits of dairy cattle, considering the simulated population structures, the trait variances and covariances assumed, sequential culling, etc. The findings are also applicable to other groups of correlated dairy cattle traits, however, such as milk, fat and protein yields; mastitis incidence and somatic cell scores; or conformation traits like body size, capacity and stature. These groups of traits are not subject to the same sequential culling as lactation traits, but are moderately correlated within and among countries and are recorded for the same populations that have lactation traits recorded.

Traits such as milk, fat and protein yield would be well suited to the RSe strategy, since each trait is commonly reported in all countries. The number of lactation traits reported is more variable among countries, however, and lactation traits are therefore better handled with a strategy like MTi, as proposed by Sullivan and Wilton (2001).

The strategies considered can also be used for traits of livestock populations other than dairy cattle, such as for weight traits at different ages for beef cattle or sheep. Sequential culling would apply to weights recorded at different ages, although population structures would differ among livestock populations and would not always match the data simulated for the present study. Additional considerations may also be required for traits that are affected, for example, by both direct and maternal genetic effects, since maternal genetic effects were not considered in the present study.

3.7. Conclusions

When base populations were unselected, and performance and pedigree data were complete, the GAM strategy had the lowest ERP for local, foreign, imported, all and top bulls, and all countries, while CNV and NAM strategies had the highest ERP. The MTr strategy of Schaeffer (2001) achieved 88% of the reduction in ERP that was achieved between CNV2 and GAM for foreign bulls, and 99-106% of the corresponding reductions for imported and top bulls. The ERP for local bulls were within 1% among all strategies.

All strategies created country biases that disadvantaged local bulls in all countries, most notably in exporting countries. Similarly, biases on foreign scales favoured bulls born in the importing countries. These biases were not expected and will be studied further in Chapter 4.

Average true genetic merits of the top 1% of bulls, selected for predicted genetic merits on the scale of each country, were criteria measuring the efficiency of predicting genetic superiority. Differences in efficiency were small among all strategies, the largest observed difference being the equivalent of only 3 months genetic progress. The small differences were explained by very high proportions of top bulls in common among strategies, particularly among the MT strategies and GAM.

When base populations were selected, country differences existed and base generation sires were above average for the within-country selection criteria. Selected base populations affected the relative ERP of GAM, which were higher than for MT strategies ($P < .05$) for foreign, top and all bulls when semen exchange was low, and top bulls when semen exchange was moderate. The GAM was the most sensitive strategy, for ERP of sires, to violation of the no-selection assumption implied with the MME, and to the levels of

semen exchange among countries. The ERP for GAM were larger than other strategies only because of differences in country biases, which were largest for the GAM strategy. The biases for all strategies were larger with selected than unselected base populations, and with lower levels of semen exchange.

Differences in efficiency of predicting genetic superiority, when base populations were selected, were similar to the corresponding differences when base populations were unselected. The differences were small, and could again be explained by very high proportions of top bulls in common among the strategies.

For both unselected and selected base populations, MACE strategies were generally similar for ERP, bias and efficiency of predicting genetic superiority, within each strategy class and between RSe and strategies in the MT class. The ERP for foreign, imported, all and top bulls, and all countries, were lower for RSe and MT strategies than for ST strategies.

International genetic evaluation strategies should be preferred for comparisons of bulls from multiple countries over strategies that rely on linear conversions of first-country national evaluations to foreign country scales or second-country national evaluations. The ERP advantages of an international animal model strategy over national evaluation strategies can be almost fully and much more simply achieved with a comparable MACE strategy. MACE strategies that accommodate multiple traits per country should be preferred over strategies that allow only one trait per country, based on ERP.

4. GENETIC EVALUATION STRATEGIES ACCOUNTING FOR SELECTION

The traditional genetic evaluation strategies considered in Chapter 3 created country biases that favoured importing country bulls on the scales of exporting countries. The country biases were larger if base populations were selected, but were also present when base populations were unselected and all performance data and pedigree, back to the base generation, were used to form the MME. These biases may have been caused by selection that was practiced within and between countries after the base generation.

Efforts to account for selection in a genetic evaluation strategy should focus, at least initially, on parental selection effects (Schaeffer et al., 1998). Parental selection effects should have been accounted for, with the traditional strategies of Chapter 3 when base populations were unselected, following the single-trait simulation results of Sorensen and Kennedy (1984). The present study included multiple traits, however, and also sequential selection of lactation traits and non-random mating. Additionally, genetic group effects were treated as random rather than fixed effects for all of the MACE and GAM strategies.

The country biases seemed to be related to the genetic group solutions, which were implicitly constrained in the MME under the groups-random model. Fries (1998) questioned the implied constraints on animal solutions in MME, suggesting that they “may not make sense”, even when the assumption of no selection is true. These implied constraints were therefore studied in more detail in the current chapter of the thesis.

4.1. Implied Constraints in MME

The multiple-trait linear mixed model can be written as;

$$\mathbf{y} = \mathbf{X}_0\mathbf{m} + \mathbf{X}_1\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of observations for all traits, $\mathbf{m}$ are overall fixed mean effects for each trait, $\mathbf{b}$ includes all additional fixed effects and $\mathbf{u}$ includes all random effects. The $\mathbf{X}_0$, $\mathbf{X}_1$ and $\mathbf{Z}$ are incidence matrices connecting observations to effects in the model. The mixed model equations (MME) are then;

$$\begin{bmatrix} \mathbf{X}_0'\mathbf{R}^{-1}\mathbf{X}_0 & \mathbf{X}_0'\mathbf{R}^{-1}\mathbf{X}_1 & \mathbf{X}_0'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{X}_0 & \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{X}_1 & \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X}_0 & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X}_1 & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_0'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

where $\mathbf{G}$ and $\mathbf{R}$ are covariance matrices for $\mathbf{u}$ and $\mathbf{e}$, respectively. Manipulation of the MME, as shown below, will reveal the constraints that are implied within.

The first critical note is that elements of any row of $\mathbf{Z}$ (column of $\mathbf{Z}'$) sum to a constant c_i that equals the number of random effects in the model for trait i , and individual elements that are not linked to observations are zero. Now, define a matrix $\mathbf{L} = \mathbf{I} \otimes \mathbf{1}$, where $\mathbf{I}$ is the identity matrix of order equal to the number of traits and $\mathbf{1}$ is a column vector of ones with order equal to the number of animals evaluated. Matrix $\mathbf{L}$ corresponds to an ordering of the solutions in $\mathbf{u}$ that is animals within traits.

$$\mathbf{L}'\mathbf{Z}' = \begin{bmatrix} \mathbf{c}_1\mathbf{1}_1' & \mathbf{0} & \cdots & \mathbf{0} \\ \mathbf{0} & \mathbf{c}_2\mathbf{1}_2' & & \mathbf{0} \\ \vdots & & \ddots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{c}_t\mathbf{1}_t' \end{bmatrix} = \mathbf{C}\mathbf{X}_0'$$

Pre-multiplying the $\mathbf{m}$ equations of the MME by $\mathbf{C}$ and the $\mathbf{u}$ equations by $\mathbf{L}'$, then substituting $\mathbf{L}'\mathbf{Z}' = \mathbf{C}\mathbf{X}_0'$, the MME become;

$$\begin{bmatrix} \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{X}_0 & \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{X}_1 & \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{X}_0 & \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{X}_1 & \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{X}_0 & \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{X}_1 & \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{L}'\mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{X}_1'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

The implied constraints in the MME are now revealed as $\mathbf{L}'\mathbf{G}^{-1}\mathbf{u}=\mathbf{0}$. This equality is implied because the $\mathbf{m}$ and $\mathbf{u}$ equations have the same right-hand-sides ($\mathbf{CX}_0'\mathbf{R}^{-1}\mathbf{y}$), and must therefore also have the same left-hand-sides. Similar manipulations for the $\mathbf{b}$ equations would reveal dependencies between the $\mathbf{m}$ and $\mathbf{b}$ equations that make the MME singular (i.e. having no unique solution). The equations for all effects in the model have dependencies with the mean equations, but for random effects these dependencies are eliminated by the implied constraints in $\mathbf{L}'\mathbf{G}^{-1}\mathbf{u}=\mathbf{0}$.

Interpretation of the implied constraints depends on the structure of $\mathbf{G}^{-1}$. This matrix is diagonal for models with independent random effects, each having independent levels, and for each effect is a constant times the identity matrix if variances are equal for all levels. For these relatively simple models the implied constraints force the average solutions for each random effect to equal zero for each trait.

For MME that include random animal ($\mathbf{a}$) effects, the levels are usually not independent because of genetic relationships among animals. With an ordering of solutions in $\mathbf{u}$ that is traits within animals rather than animals within traits, $\mathbf{G}^{-1} = \mathbf{A}^{-1} \otimes \mathbf{G}_{(t)}^{-1}$ and the corresponding definition for a re-ordered matrix $\mathbf{L} = \mathbf{1} \otimes \mathbf{I}$. The implied constraints on the animal equations are therefore $\mathbf{1}'\mathbf{A}^{-1} \otimes \mathbf{G}_{(t)}^{-1} \hat{\mathbf{a}} = \mathbf{0}$, which is equivalent to the sum of base generation animal solutions being zero for each trait. This equivalence is due to the structure of $\mathbf{A}^{-1}$, which has column sums equal to zero for all animals with identified parentage, and column sums equal to 1 for animals with unknown parents (i.e. the base generation animals).

For models with genetic groups (**g**) that are treated as fixed effects, a QP-transformation (Quaas and Pollak, 1981) of the MME to simplify derivation of animal EBV resulted in a new matrix **W** (Westell et al., 1988) that replaced **A**⁻¹ in the MME. The QP-transformation combined genetic group and animal solutions that contribute to an animal's breeding value (**Qg+a**) allowing for direct solving of animal EBV (**Qĝ + â**). Without the QP-transformation, group and animal solutions had to be combined as a second step after solving for **g** and **a** separately. The QP-transformed MME were described for a single-trait model with random animal effects, fixed genetic group effects plus an additional fixed effect, and can be similarly described for multiple-trait models. For a multiple-trait model with only fixed genetic group effects in **b**, for example, the QP-transformed MME would have the following form;

$$\begin{bmatrix} \mathbf{X}_0' \mathbf{R}^{-1} \mathbf{X}_0 & \mathbf{0} & \mathbf{X}_0' \mathbf{R}^{-1} \mathbf{Z} \\ \mathbf{0} & \mathbf{0} + \mathbf{W}_{11} \otimes \mathbf{G}_{(n)}^{-1} & \mathbf{0} + \mathbf{W}_{12} \otimes \mathbf{G}_{(n)}^{-1} \\ \mathbf{Z}' \mathbf{R}^{-1} \mathbf{X}_0 & \mathbf{0} + \mathbf{W}_{21} \otimes \mathbf{G}_{(n)}^{-1} & \mathbf{Z}' \mathbf{R}^{-1} \mathbf{Z} + \mathbf{W}_{22} \otimes \mathbf{G}_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{g} \\ \mathbf{Qg} + \mathbf{a} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_0' \mathbf{R}^{-1} \mathbf{y} \\ \mathbf{0} \\ \mathbf{Z}' \mathbf{R}^{-1} \mathbf{y} \end{bmatrix}$$

Letting **Z**_{*} = [**0 Z**] and **u** = $\begin{pmatrix} \mathbf{g} \\ \mathbf{Qg} + \mathbf{a} \end{pmatrix}$, the QP-transformed MME can also be written as;

$$\begin{bmatrix} \mathbf{X}_0' \mathbf{R}^{-1} \mathbf{X}_0 & \mathbf{X}_0' \mathbf{R}^{-1} \mathbf{Z}_* \\ \mathbf{Z}_*' \mathbf{R}^{-1} \mathbf{X}_0 & \mathbf{Z}_*' \mathbf{R}^{-1} \mathbf{Z}_* + \mathbf{W} \otimes \mathbf{G}_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_0' \mathbf{R}^{-1} \mathbf{y} \\ \mathbf{Z}_*' \mathbf{R}^{-1} \mathbf{y} \end{bmatrix}$$

Matrix **Q** links animals to genetic groups, and **W** incorporates and has a structure similar to **A**⁻¹. The dimensions of **W** are equal to the number of animals plus the number of groups, whereas the dimensions of **A**⁻¹ are equal to the number of animals only. All column sums of **W** are equal to zero (**1'W=0**) and there are no implied constraints on the group or animal solutions in these QP-transformed MME, because **1'W**⊗**G**_(n)⁻¹**u** = **0** for any **u**. Dependencies will exist between genetic groups and the means (**m**) and any other fixed

effects that are added to the above model, which directly affects the animal solutions since they now include functions of the group solutions (Qg).

These dependencies are eliminated if groups are treated as random effects by adding quantities to the group diagonals of W_{11} , for example adding an identity matrix (Schaeffer, 1994);

$$W^* = \begin{bmatrix} W_{11} & W_{12} \\ W_{21} & W_{22} \end{bmatrix} + \begin{bmatrix} I & 0 \\ 0 & 0 \end{bmatrix} \quad \text{and} \quad 1'W^* = [1' \ 0]$$

Then $1'W^* \otimes G_{(n)}^{-1}u = 0$ simplifies to $1' \otimes G_{(n)}^{-1}g = 0$. These constraints are equivalent to the sum of all genetic group solutions being zero for each trait. The transformed MME with groups and animals as random effects can be written as;

$$\begin{bmatrix} X_0'R^{-1}X_0 & X_0'R^{-1}Z. \\ Z.'R^{-1}X_0 & Z.'R^{-1}Z. + W^* \otimes G_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} m \\ u \end{bmatrix} = \begin{bmatrix} X_0'R^{-1}y \\ Z.'R^{-1}y \end{bmatrix}$$

4.2. Implied Constraints in the MME used for MACE

All MACE models considered in the present study included one random sire effect (s), and although genetic groups were a second random effect in the model, all Z_* matrices had row sums equal to one because $Z_* = [0 \ Z]$. Hence, $C=I$ and $L'Z_*' = X_0'$. The QP-transformed MME, substituting $L'Z_*'$ for X_0' are;

$$\begin{bmatrix} L'Z_*'R^{-1}Z.L & L'Z_*'R^{-1}Z. \\ Z.'R^{-1}Z.L & Z.'R^{-1}Z. + W^* \otimes G_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} m \\ u \end{bmatrix} = \begin{bmatrix} L'Z_*'R^{-1}y \\ Z.'R^{-1}y \end{bmatrix}$$

with $u = \begin{pmatrix} g \\ Qg + s \end{pmatrix}$. For MACE, $Z_*'R^{-1}Z_*$ is approximated by a diagonal matrix D of weighting factors or blocks, and $Z_*'R^{-1}y$ is approximated by Dy . The MME used for MACE can therefore be written as;

$$\begin{bmatrix} \mathbf{L}'\mathbf{D}\mathbf{L} & \mathbf{L}'\mathbf{D} \\ \mathbf{D}\mathbf{L} & \mathbf{D} + \mathbf{W}' \otimes \mathbf{G}_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{L}'\mathbf{D}\mathbf{y} \\ \mathbf{D}\mathbf{y} \end{bmatrix}$$

which are equivalent to

$$\begin{bmatrix} \mathbf{L}'\mathbf{D}\mathbf{L} & \mathbf{L}'\mathbf{D} + \mathbf{1}'\mathbf{W}' \otimes \mathbf{G}_{(n)}^{-1} \\ \mathbf{D}\mathbf{L} & \mathbf{D} + \mathbf{W}' \otimes \mathbf{G}_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{L}'\mathbf{D}\mathbf{y} \\ \mathbf{D}\mathbf{y} \end{bmatrix}$$

under the constraints in $\mathbf{1}'\mathbf{W}' \otimes \mathbf{G}_{(n)}^{-1}\mathbf{u} = \mathbf{0}$, which are the same as in $\mathbf{1}' \otimes \mathbf{G}_{(n)}^{-1}\mathbf{g} = \mathbf{0}$, or

equivalently for each trait j , $\sum_{k=1}^{ng} \hat{g}_{kj} = 0$ for ng genetic groups.

The equations for the mean effects ($\mathbf{m}$) are equal to trait sums of the $\mathbf{u}$ equations, subject to the implied constraints on sub-vector $\mathbf{g}$ within $\mathbf{u}$. Conceivably, any set of constraints could be placed on $\mathbf{u}$ to derive $\mathbf{m}$, but the implied constraints are expected to minimize ERP of $\mathbf{u}$ (Henderson, 1984) when model assumptions are valid.

Each solution in sub-vector $\mathbf{Qg} + \mathbf{s}$ of $\mathbf{u}$ includes a weighted average of the genetic group solutions, with weights summing to one (Westell et al., 1988). Therefore, any change that affects genetic group solutions also has direct implications for the sire solutions in $\mathbf{Qg} + \mathbf{s}$. The predicted breeding values (EBV) of sires in MACE are sums of sire solutions in $\mathbf{Qg} + \mathbf{s}$ plus corresponding trait means in $\mathbf{m}$ (Schaeffer, 1994).

If genetic groups were treated as fixed, there would be complete dependency between the genetic group and mean equations. The mean equations could then be ignored, or alternatively the average group solutions constrained to equal a fixed value, zero for example. The sum of means and fixed genetic group solutions would be invariant to the choice of constraints, but only for group effects connected to observations. Group effects not connected to observations would be non-estimable under the fixed groups model, and

EBV for all sires connected to those group effects, through Qg , would therefore also be non-estimable.

Under a MACE model with fixed genetic groups, maternal granddam group solutions for the most recent time period would only be estimable in one country, unless young bulls were sampled simultaneously in multiple countries. This would make comparisons of young bulls from different countries, which are of considerable interest, non-estimable. Additionally, many comparisons of animals from pairs of countries that are not well connected would also be non-estimable.

All sire comparisons are estimable when group effects are treated as random, but the accuracy of the comparisons are subject to the validity of the implied constraints ($1' \otimes G^{-1} g = 0$). There is an implied assumption, with the constraints imposed by using W^* , that all base generation groups are unrelated and unselected. This assumption is almost certainly invalid since group effects are in the model to account for selection, and in particular to account for genetic trends.

The average of all group solutions is higher than the average of base generation group solutions when genetic trends are positive. Therefore, constraints on all groups rather than the base generation groups create lower solutions for u , and correspondingly higher solutions for m . In MACE, the consequences of this shift are significant because the solutions in m are the starting point for parent average evaluations of foreign bulls.

Foreign bulls without local evaluations receive, for their MACE evaluations, the sum of their local parent average solutions and the conversion of their foreign-scale Mendelian sampling solutions (Klei, 1995; Mrode and Swanson, 1999). Animals with local evaluations, however, receive MACE evaluations that basically reflect their local proof,

regardless of solutions for m . Changes to the parental average therefore directly affect comparisons of foreign relative to local bulls. The biases observed in Chapter 3 favoured bulls from importing countries over local bulls on the evaluation scales of exporting countries, which suggests that the m solutions on the scales of exporting countries may have been too high with the traditional MACE strategies.

An alternative to the traditional implied constraints was therefore considered for the MACE* strategies, by forcing only base generation group solutions to sum to zero rather than all group solutions. For the traditional NAM and GAM strategies, all genetic groups had only base generation descendents because complete pedigree information was used to form W^* . The pedigree used for MACE, however, excluded female ancestors and W^* included maternal grandsire and maternal granddam groups with descendents in all years of the simulation. Alternative constraints for NAM or GAM may be to force average solutions of zero on local groups only, only the groups with male descendents or only the groups with female descendents, but alternatives such as these were not considered for the present study.

4.3. Materials and methods

4.3.1. Data

Simulated data for populations with moderate levels of semen exchange, which were used to study the traditional MME-based strategies (Chapter 3), were also used to study the selection-modified MACE strategies.

4.3.2. Selection-modified MME for MACE

The $\mathbf{m}$ equations of the MME served only to impose the implied constraints, which we now wish to change. The $\mathbf{m}$ equations could not be easily modified to impose different constraints and were therefore ignored for the selection-modified MACE strategies (MACE*). The MME, ignoring the $\mathbf{m}$ equations are;

$$\begin{bmatrix} \mathbf{DL} & \mathbf{D} + \mathbf{W}^* \otimes \mathbf{G}_{(n)}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{m} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{Dy} \end{bmatrix}$$

The number of equations was equal to the number of solutions in $\mathbf{u}$ (n_u), and therefore less than the number of unknowns, which was n_u plus the number of solutions in $\mathbf{m}$. There was one solution per trait in $\mathbf{m}$, so one constraint was required per trait to derive solutions for both $\mathbf{m}$ and $\mathbf{u}$. The following iterative scheme was used to solve for $\mathbf{m}$ and $\mathbf{u}$, subject to the desired set of constraints;

1. $i = 0$; $\hat{\mathbf{m}}^{(i)} = 0$; $\hat{\mathbf{u}}^{(i)} = 0$
2. $i = i + 1$; Compute $\hat{\mathbf{u}}^{(i)}$ given $\hat{\mathbf{m}}^{(i-1)}$ and $\hat{\mathbf{u}}^{(i-1)}$ by Gauss-Seidel iteration.
3. Compute the average group solutions that must be zero at convergence to impose the desired constraints, i.e. for each trait j compute $x_j = \frac{1}{n} \sum_{k=1}^n \hat{\mathbf{g}}_{kj}^{(i)}$ for the n groups included in the constraint.
4. For each trait j , compute $ADJ_j = x_j * relax$, setting $relax < 1.0$ if necessary to ensure convergence.
5. For each trait j , $\hat{\mathbf{u}}_j^{(i)} = \hat{\mathbf{u}}_j^{(i-1)} - ADJ_j$, $\hat{\mathbf{m}}_j^{(i)} = \hat{\mathbf{m}}_j^{(i-1)} + ADJ_j$.
6. Until converged, go to step 2. The solutions are converged when $x_j = 0$ for each trait and $\hat{\mathbf{u}}^{(i)} = \hat{\mathbf{u}}^{(i-1)}$, to an acceptable degree of precision.

The validity of ignoring the $\mathbf{m}$ equations and applying the constraints directly on $\mathbf{u}$ was first tested with the traditional constraints that all groups have average trait solutions of zero (all groups were included to compute x_j). The solutions for $\mathbf{u}$, using the traditional constraints with this new approach, were invariably equal to the solutions derived by the traditional approach. The traditional approach was to solve the complete MACE equations that included both $\mathbf{m}$ and $\mathbf{u}$ using Gauss-Seidel iteration. The number of iterations required was often doubled, however, for the new relative to the traditional approach.

Once validated, the new approach was applied for selection-modified MACE* strategies corresponding to each of the traditional MACE strategies studied in Chapter 3. With MACE*, only base generation groups were included to compute x_j . Convergence for the MACE* strategies was approximately two to five times slower than for the traditional MACE strategies, and under-relaxation to impose the constraints ($relax < 1.0$) was sometimes required to guarantee convergence when multiple traits were included for each country.

4.3.3. Criteria for Comparisons of Strategies

The criteria used to compare selection-modified MACE* strategies were the same as those used for the traditional MACE strategies, as described in Chapter 3.

4.4. Results and Discussion

4.4.1. Errors of Prediction

The GAM had lower ERP for local bulls than all of the selection-modified MACE* strategies ($P<.01$), and lower ERP for imported bulls for most of the MACE* strategies ($P<.01$), when base populations were unselected (Table 26). The ERP differences for these two groups of bulls were similar to the corresponding differences for MACE (Table 14 in Chapter 3). For foreign and all bulls ($P<.01$) and top bulls ($P<.10$), however, GAM had higher ERP than MACE*, whereas ERP were lower for GAM than MACE.

With selected base populations, differences in ERP for local and imported bulls, between MACE* strategies and GAM were again similar to the differences observed between MACE and GAM in Chapter 3. The ERP were much lower relative to GAM, however, for the MACE* strategies, for foreign, all and top bulls. The corresponding differences for MACE strategies were much smaller. For example, the differences in ERP between MTi* and GAM for foreign, all and top bulls were -0.042, -0.032 and -0.023 (Table 26), compared with corresponding differences between MTi and GAM of -0.003, -0.002 and -0.010 (Table 14). The relative reductions in ERP, dividing by the ERP for GAM, were 6.4%, 5.3% and 3.9% for MTi*, compared with 0.5%, 0.5% and 1.7% for MTi. When semen exchange was low, the relative reductions for MTi* (not shown) were 10.2%, 8.6% and 7.5%, compared with 2.6%, 2.2% and 3.5% for MTi (derived from Table 15).

The relative effects of different weighting factors within a class of MACE* strategies were small and consistent with the corresponding effects observed within each class of traditional MACE strategies in Chapter 3. The bulls most affected were the imported bulls. The ERP were generally lower if Ne were used instead of ND as weighting factors for strategies in the ST* and RS* classes, and ERP were lowest for MTr* among all MACE* strategies, with both unselected and selected base populations.

The ERP for all bulls, for MACE* strategies relative to GAM, were reduced most notably on the scales of exporting countries (Table 27). The ERP on the scales of importing countries were not different ($P>.05$) from GAM for any of the RS* or MT* strategies when base populations were selected, and were essentially equal to what they had been for the corresponding RS and MT strategies (Table 16). There were slight reductions in ERP on the scales of importing countries switching from MACE to MACE* strategies, if base populations were selected, but the reductions were small in comparison to the reductions observed on the scales of exporting countries.

Strategies in the RS* or MT* classes had ERP for all bulls that were 7.6% and 9.7-10.5% lower ($P<.01$) than GAM, on scales EXP1 and EXP2 respectively, when base populations were selected and levels of semen exchange were moderate (derived from Table 27). When semen exchange was low, reductions in ERP for foreign, all and top bulls using strategy MTi* instead of GAM (not shown) were 14.8%, 11.5% and 11.1% on scale EXP1, and 16.5%, 14.8% and 13.5% on scale EXP2.

The ERP for any group of bulls included the square of the average bias for the group, relative to local bulls, which will be considered in greater detail in the general discussion section below. This bias would be largest for foreign bulls since they did not

have progeny data on the local scale for comparisons with local bulls. Reductions in ERP switching from MACE to MACE* strategies were largest for foreign bulls.

Table 26. Differences in ERP^z, and ERP for GAM, for overall merit across evaluation scales of all countries, for different groups of bulls, with moderate levels of semen exchange among countries, for selection-modified MACE* strategies (t-value in parentheses).

Strategies ^y	Bulls included				
	Local	Foreign	Imported	All	Top ^w
Unselected base populations					
STn*-GAM	0.003 (4.5)	0.006 (3.3)	0.016 (5.3)	0.006 (3.7)	-0.003 (-0.3)
STe*-GAM	0.003 (4.6)	0.006 (3.2)	0.013 (4.6)	0.005 (3.6)	-0.006 (-0.6)
RSn*-GAM	0.004 (6.2)	-0.011 (-6.5)	0.051 (7.1)	-0.007 (-5.0)	0.008 (1.5)
RSe*-GAM	0.003 (4.7)	-0.012 (-8.2)	0.004 (1.6)	-0.008 (-7.4)	-0.018 (-2.9)
MTr*-GAM	0.003 (4.4)	-0.011 (-8.3)	0.001 (0.4)	-0.008 (-7.6)	-0.016 (-2.5)
MTn*-GAM	0.003 (4.4)	-0.010 (-7.3)	0.005 (2.2)	-0.007 (-6.6)	-0.012 (-1.7)
MTe*-GAM	0.003 (4.5)	-0.009 (-6.6)	0.018 (4.8)	-0.007 (-5.7)	-0.010 (-1.4)
MTi*-GAM	0.003 (4.5)	-0.010 (-6.9)	0.012 (3.9)	-0.007 (-6.1)	-0.011 (-1.7)
GAM	0.466 ± 0.002	0.615 ± 0.003	0.289 ± 0.004	0.574 ± 0.003	0.579 ± 0.010
Selected base populations					
STn*-GAM	0.003 (4.9)	-0.025 (-7.5)	0.010 (3.9)	-0.018 (-7.1)	-0.014 (-2.0)
STe*-GAM	0.003 (5.4)	-0.024 (-7.4)	0.010 (3.8)	-0.018 (-7.0)	-0.016 (-2.3)
RSn*-GAM	0.006 (8.3)	-0.041 (-14.2)	0.048 (5.5)	-0.030 (-12.9)	-0.011 (-1.6)
RSe*-GAM	0.003 (5.7)	-0.041 (-14.2)	0.003 (1.2)	-0.031 (-13.6)	-0.026 (-5.6)
MTr*-GAM	0.003 (5.1)	-0.042 (-14.2)	-0.005 (-3.1)	-0.032 (-13.6)	-0.026 (-5.4)
MTn*-GAM	0.003 (4.5)	-0.042 (-13.3)	-0.002 (-0.9)	-0.032 (-12.8)	-0.024 (-4.3)
MTe*-GAM	0.002 (4.2)	-0.041 (-13.0)	0.009 (2.9)	-0.032 (-12.5)	-0.021 (-4.1)
MTi*-GAM	0.003 (4.7)	-0.042 (-13.2)	0.004 (1.6)	-0.032 (-12.7)	-0.023 (-4.1)
GAM	0.463 ± 0.002	0.659 ± 0.005	0.299 ± 0.005	0.608 ± 0.004	0.591 ± 0.010

^zERP included prediction error variance and prediction bias relative to all local bulls.

^wtop 10 evaluated bulls from each country.

^yStrategies are described in Table 1.

*Base generation, instead of all, genetic group solutions constrained to have average solutions of zero.

Table 27. Differences in ERP, and ERP for GAM, for overall merit of all bulls, by country of evaluation, with moderate levels of semen exchange among countries, for selection-modified MACE* strategies (t-value in parentheses).

Strategies	Country of evaluation			
	EXP1	EXP2	IMP1	IMP2
Unselected base populations				
STn*-GAM	-0.004 (-1.3)	-0.006 (-1.2)	0.021 (7.2)	0.011 (4.2)
STe*-GAM	-0.004 (-1.2)	-0.006 (-1.3)	0.021 (7.2)	0.010 (4.3)
RSn*-GAM	-0.011 (-3.1)	-0.017 (-4.6)	0.002 (1.0)	0.000 (0.2)
RSe*-GAM	-0.012 (-3.6)	-0.019 (-4.8)	0.001 (0.7)	-0.004 (-1.9)
MTr*-GAM	-0.012 (-3.3)	-0.019 (-4.6)	0.001 (0.5)	-0.003 (-1.5)
MTn*-GAM	-0.011 (-3.3)	-0.018 (-4.2)	0.002 (1.1)	-0.002 (-1.0)
MTe*-GAM	-0.011 (-3.2)	-0.017 (-3.9)	0.003 (1.5)	-0.001 (-0.4)
MTi*-GAM	-0.011 (-3.2)	-0.017 (-4.0)	0.003 (1.4)	-0.001 (-0.6)
GAM	0.550 ± 0.004	0.594 ± 0.004	0.575 ± 0.005	0.576 ± 0.005
Selected base populations				
STn*-GAM	-0.042 (-8.7)	-0.054 (-8.0)	0.011 (4.9)	0.013 (3.7)
STe*-GAM	-0.042 (-8.8)	-0.053 (-8.0)	0.010 (4.8)	0.014 (3.7)
RSn*-GAM	-0.046 (-10.1)	-0.064 (-11.3)	-0.005 (-3.3)	-0.002 (-0.5)
RSe*-GAM	-0.046 (-10.2)	-0.065 (-10.9)	-0.006 (-3.5)	-0.005 (-1.9)
MTr*-GAM	-0.046 (-9.9)	-0.068 (-11.2)	-0.006 (-3.2)	-0.006 (-2.4)
MTn*-GAM	-0.046 (-9.4)	-0.069 (-10.9)	-0.005 (-2.5)	-0.005 (-2.2)
MTe*-GAM	-0.046 (-9.3)	-0.069 (-10.6)	-0.004 (-2.1)	-0.005 (-2.0)
MTi*-GAM	-0.046 (-9.5)	-0.069 (-10.7)	-0.004 (-2.4)	-0.005 (-2.0)
GAM	0.602 ± 0.007	0.659 ± 0.009	0.579 ± 0.003	0.588 ± 0.004

*Base generation, instead of all, genetic group solutions constrained to have average solutions of zero.

4.4.2. Fairness of Country Comparisons

Local bulls were unbiased ($P > .05$) in comparisons with foreign bulls with the selection-modified MACE* strategies and unselected base populations (Table 28). Corresponding biases against local bulls with the traditional MACE strategies, particularly on exporting country scales (Table 18), were therefore eliminated by switching to MACE*. The local bull biases in exporting countries with MACE were not eliminated with MACE* when base populations were selected ($P < .01$), but were reduced by approximately 50%, ranging from -0.122 to -0.148 for MACE* (Table 28) compared with a range of -0.259 to -0.292 for MACE (Table 18).

Advantages, in terms of reduced bias for MACE* relative to MACE, were also observed on foreign scales of evaluation, consistent with the bias reductions observed for local bulls. Bulls from all countries had unbiased evaluations on foreign scales ($P > .05$) with MACE* and unselected base populations (Table 29). Bulls from exporting countries also had unbiased foreign scale evaluations ($P > .10$) when base populations were selected. Foreign scale biases for bulls from importing countries ranged from 0.169 to 0.219 for MACE* (Table 29), about 50% smaller than the corresponding differences for MACE, which ranged from 0.335 to 0.395 (Table 20).

Table 28. Bias on the local scale, for overall merit of all bulls, with moderate levels of semen exchange among countries, for selection-modified MACE* strategies (t-value in parentheses).

Strategy	Country of birth			
	EXP1	EXP2	IMP1	IMP2
Unselected base populations				
STn*	0.022 (1.3)	0.007 (0.3)	-0.059 (-2.0)	0.024 (1.1)
STe*	0.024 (1.4)	0.004 (0.2)	-0.060 (-2.1)	0.015 (0.7)
RSn*	0.007 (0.4)	-0.019 (-1.1)	-0.056 (-2.1)	-0.044 (-2.3)
RSe*	0.001 (0.0)	-0.025 (-1.3)	-0.048 (-1.8)	-0.005 (-0.3)
MTr*	0.017 (1.0)	-0.010 (-0.5)	-0.039 (-1.5)	0.001 (0.1)
MTn*	0.017 (0.9)	-0.006 (-0.3)	-0.037 (-1.4)	0.005 (0.2)
MTe*	0.018 (1.0)	-0.002 (-0.1)	-0.033 (-1.2)	0.018 (0.9)
MTi*	0.019 (1.0)	-0.004 (-0.2)	-0.036 (-1.3)	0.013 (0.6)
GAM	-0.137 (17.7)	-0.171 (-9.9)	-0.068 (-3.1)	-0.061 (-2.7)
Selected base populations				
STn*	-0.128 (-10.2)	-0.140 (-6.3)	-0.019 (-0.9)	-0.043 (-1.7)
STe*	-0.125 (-10.0)	-0.148 (-6.7)	-0.018 (-0.9)	-0.054 (-2.1)
RSn*	-0.131 (-10.0)	-0.150 (-7.2)	-0.010 (-0.5)	-0.056 (-2.3)
RSe*	-0.135 (-10.1)	-0.147 (-6.9)	-0.004 (-0.2)	-0.028 (-1.2)
MTr*	-0.129 (-9.8)	-0.136 (-6.5)	0.005 (0.2)	-0.019 (-0.8)
MTn*	-0.128 (-9.8)	-0.128 (-6.0)	0.007 (0.3)	-0.016 (-0.7)
MTe*	-0.126 (-9.4)	-0.122 (-5.5)	0.009 (0.4)	-0.008 (-0.4)
MTi*	-0.124 (-9.2)	-0.127 (-5.7)	0.007 (0.3)	-0.013 (-0.6)
GAM	-0.296 (-17.2)	-0.329 (-16.8)	0.006 (0.3)	-0.013 (-0.6)

*Base generation, instead of all, genetic group solutions constrained to have average solutions of zero.

Table 29. Bias on foreign country scales, for overall merit of all bulls, with moderate levels of semen exchange among countries, for selection-modified MACE* strategies (t-value in parentheses).

Strategy	Country of birth			
	EXP1	EXP2	IMP1	IMP2
Unselected base populations				
STn*	0.027 (1.3)	-0.004 (-0.3)	-0.059 (-2.6)	0.026 (1.0)
STe*	0.034 (1.6)	0.000 (0.0)	-0.057 (-2.6)	0.022 (0.9)
RSn*	0.056 (2.7)	0.015 (1.0)	-0.009 (-0.4)	0.034 (1.6)
RSe*	0.030 (1.5)	-0.009 (-0.6)	0.003 (0.1)	0.049 (2.2)
MTr*	0.027 (1.3)	-0.014 (-0.9)	-0.020 (-1.0)	0.027 (1.2)
MTn*	0.023 (1.1)	-0.015 (-1.0)	-0.023 (-1.1)	0.026 (1.1)
MTe*	0.012 (0.6)	-0.023 (-1.5)	-0.024 (-1.1)	0.028 (1.2)
MTi*	0.017 (0.8)	-0.020 (-1.3)	-0.024 (-1.1)	0.027 (1.2)
GAM	0.076 (4.0)	0.004 (0.3)	0.181 (11.8)	0.200 (9.8)
Selected base populations				
STn*	0.009 (0.5)	-0.009 (-0.6)	0.217 (7.4)	0.174 (7.1)
STe*	0.018 (1.1)	-0.007 (-0.5)	0.219 (7.6)	0.169 (6.9)
RSn*	0.024 (1.5)	-0.004 (-0.2)	0.199 (7.9)	0.177 (7.0)
RSe*	0.002 (0.1)	-0.021 (-1.4)	0.205 (8.2)	0.185 (7.4)
MTr*	-0.009 (-0.5)	-0.024 (-1.6)	0.196 (7.8)	0.174 (7.2)
MTn*	-0.014 (-0.8)	-0.023 (-1.5)	0.189 (7.5)	0.170 (7.1)
MTe*	-0.021 (-1.3)	-0.028 (-1.8)	0.187 (7.3)	0.171 (7.1)
MTi*	-0.016 (-0.9)	-0.027 (-1.8)	0.189 (7.4)	0.170 (7.0)
GAM	0.015 (1.0)	-0.045 (-3.1)	0.391 (15.3)	0.367 (14.0)

*Base generation, instead of all, genetic group solutions constrained to have average solutions of zero.

4.4.3. Efficiency of Predicting Genetic Superiority

The average true genetic merits of top bulls, selected by each strategy, were not significantly different ($P > .10$) for the selection-modified MACE* strategies relative to GAM (Table 30) for either unselected or selected base populations. The small differences from GAM for MACE* were very similar to the corresponding differences observed previously for the traditional MACE strategies (Table 22). Expected genetic progress would therefore be very similar using traditional MACE, selection-modified MACE* or GAM strategies to compute international genetic evaluations of sires, ignoring factors such as global population structures, inbreeding, etc. that may be affected differently by each strategy.

Despite large advantages for MACE* in terms of smaller ERP for many groups of bulls and smaller country biases on exporting country scales, tendencies were for lower true genetic merits of top bulls selected by MACE* rather than GAM. These tendencies may be explained by the fact that local bulls generally had a better chance of being among the top selected bulls because of genetic correlations among countries that were less than unity. Local bulls had the lowest ERP with GAM for all simulations, so the top local bulls identified by GAM may have had higher true genetic merits than the top local bulls identified by MACE or MACE* strategies. The local bull ERP for MACE strategies were closer to NAM than GAM (Tables 14) and, being slightly higher for MACE* (Table 26) than MACE, were even closer to NAM for MACE*.

Table 30. Differences in true overall merit, for top^z 10 evaluated bulls from each country, by country of evaluation, with moderate levels of semen exchange among countries (t-value in parentheses).

Strategies	Country of evaluation				
	EXP1	EXP2	IMP1	IMP2	All ^w
Unselected base populations					
STn*-GAM	-0.012 (-1.2)	-0.005 (-0.5)	-0.022 (-1.8)	-0.010 (-0.8)	-0.012 (-1.9)
STe*-GAM	-0.012 (-1.2)	-0.008 (-0.6)	-0.020 (-1.9)	-0.009 (-0.9)	-0.012 (-2.0)
RSn*-GAM	-0.014 (-2.0)	-0.005 (-0.8)	-0.011 (-2.3)	-0.009 (-0.9)	-0.010 (-2.2)
RSe*-GAM	0.000 (0.0)	0.012 (1.6)	-0.005 (-0.6)	0.006 (0.9)	0.003 (0.8)
MTr*-GAM	-0.002 (-0.3)	0.005 (1.0)	-0.009 (-1.3)	0.003 (0.4)	-0.001 (-0.2)
MTn*-GAM	-0.005 (-0.7)	0.001 (0.2)	-0.014 (-2.0)	0.007 (1.1)	-0.003 (-0.7)
MTe*-GAM	-0.002 (-0.4)	0.007 (1.2)	-0.012 (-1.6)	0.008 (0.8)	0.000 (0.1)
MTi*-GAM	-0.004 (-0.6)	0.008 (1.3)	-0.014 (-2.0)	0.009 (1.1)	0.000 (0.0)
GAM	3.289 ± 0.042	3.163 ± 0.047	3.364 ± 0.049	3.180 ± 0.047	3.249 ± 0.041
TRUE	3.667 ± 0.035	3.580 ± 0.035	3.721 ± 0.042	3.560 ± 0.042	3.632 ± 0.034
Selected base populations					
STn*-GAM	-0.004 (-0.6)	0.006 (0.6)	-0.035 (-3.1)	-0.010 (-1.1)	-0.011 (-1.9)
STe*-GAM	0.000 (0.0)	0.007 (0.8)	-0.032 (-2.8)	-0.012 (-1.4)	-0.009 (-1.7)
RSn*-GAM	-0.004 (-0.5)	-0.021 (-2.0)	-0.008 (-0.9)	-0.008 (-0.8)	-0.010 (-1.6)
RSe*-GAM	-0.003 (-0.6)	-0.003 (-0.4)	-0.006 (-0.7)	-0.009 (-1.1)	-0.005 (-1.1)
MTr*-GAM	-0.008 (-1.8)	-0.004 (-0.5)	-0.008 (-0.9)	-0.001 (-0.1)	-0.005 (-1.2)
MTn*-GAM	-0.013 (-2.0)	-0.001 (-0.1)	-0.011 (-1.2)	-0.004 (-0.5)	-0.007 (-1.5)
MTe*-GAM	-0.006 (-1.3)	0.000 (0.0)	-0.007 (-0.7)	-0.014 (-1.9)	-0.007 (-1.6)
MTi*-GAM	-0.008 (-1.6)	0.003 (0.4)	-0.007 (-0.8)	-0.008 (-1.0)	-0.005 (-1.1)
GAM	3.616 ± 0.062	3.530 ± 0.071	3.633 ± 0.065	3.485 ± 0.073	3.566 ± 0.061
TRUE	3.957 ± 0.060	3.909 ± 0.067	3.964 ± 0.067	3.895 ± 0.066	3.931 ± 0.059

*Base generation, instead of all, genetic group solutions constrained to have average solutions of zero.

4.4.4. General Discussion

The ERP reported throughout the thesis were computed after removing mean differences between genetic predictions and true genetic values for all local bulls. The local bull evaluations were therefore unbiased, but biases were not removed for other groups of bulls relative to local bulls. The ERP included any biases that remained relative to all local bulls, for example for foreign bulls. Hence, all country biases studied were included in and increased ERP for all groups except local bulls. Relative differences in ERP among strategies were strongly influenced by the relative size of country biases for each strategy.

Considering ERP as reported, when levels of semen exchange were moderate, traditional and selection-modified strategies from all classes are compared in Figure 8 for unselected and selected base populations. Multiple-trait versus single-trait per country strategies were CNV2 versus CNV1, and RS, MT or GAM versus ST for traditional strategies, and RS* or MT* versus ST* for selection-modified MACE* strategies. The multiple-trait strategies had lower ERP, without exception, for both unselected and selected base populations. Among the multiple-trait strategies, CNV2 had higher ERP and the selection-modified MACE* strategies had lower ERP, for both unselected and selected base populations. The traditional MACE (RS and MT) and GAM strategies were similar, and had intermediate ERP that were closer to MACE* when base populations were unselected and closer to CNV2 when base populations were selected.

Figure 8. ERP of overall merit for all bulls, across evaluation scales of all countries, with moderate levels of semen exchange among countries.

Considering the within-country ERP_w (described in section 3.6.3.1) adjusted to remove the effects of country biases, differences among strategies were much less than for ERP, and GAM was among the strategies with lowest ERP_w for both unselected and selected base populations (Figure 9). The GAM compared bulls as accurately or more accurately within, but less accurately between countries of origin, relative to both the traditional MACE and the selection-modified MACE* strategies.

Selection-modified GAM strategies were not considered in the present study for two reasons. Firstly, the computing time for one GAM evaluation was substantially more than for all traditional and selection-modified MACE strategies combined. Secondly, it was not clear what modifications should be made, since the modifications made for the MACE strategies would have had no effect on GAM because all genetic groups in GAM were base generation genetic groups. Fixed genetic group effects could also not be used, because all group solutions of interest would not have been estimable.

The GAM might be the preferred strategy if changes could be made (i.e. GAM*) to eliminate the country biases that were observed. Otherwise, GAM would not be preferred over the best MACE or MACE* strategies for comparisons of bulls from different countries, based on fairness of country comparisons or ERP. The MACE and MACE* strategies would always be preferred over GAM for computing ease.

Figure 9. Within-country ERP_w of overall merit for all bulls, across evaluation scales of all countries, with moderate levels of semen exchange among countries.

The modifications that were made to the MME for MACE* in the present study (i.e. changes to the constraints on group solutions) accounted for selection effects on genetic group solutions and had very large effects on country comparisons. The country comparisons, on the scales of the exporting countries in particular, were changed by as much as 0.15 genetic standard deviations. The effects were generally limited to the scales of the exporting countries, however, suggesting that the modifications were not necessary for evaluations on the scales of the importing countries. Single-trait, within-country genetic evaluation systems may also be less affected by changes to the constraints on group solutions, although this was not studied.

The proposed changes to the constraints on group solutions would be most effective in situations where data on correlated traits are observed in one data subset, only one of the traits is observed in another subset, and the unobserved trait is of interest for comparisons of all individuals. A second example for dairy cattle might be a trait like feed efficiency, which is difficult to record on all farms but could be measured at a central facility on a subset of the population. Feed efficiency could then be evaluated in a multiple-trait analysis with other traits that are recorded both at the central facility and on all farms. Animals from all herds can be evaluated for feed efficiency, but the herds contributing cows to the central facility may have biased evaluations for feed efficiency relative to herds that do not contribute cows to the central facility. This example would also apply to beef cattle or other species recording feed efficiency at central testing facilities but not on all farms. Another example for meat-animals would be carcass traits that are of interest for all animals but only measured on a subset, while the general population has records for ultrasound traits that are

correlated with the carcass traits of interest. Evaluations for carcass traits for individuals in the general population may be biased relative to individuals from the sub-population that had both ultrasound and carcass data recorded.

There were some difficulties solving the MME with the modified constraints on group solutions, and the approach that was used in the present study may not guarantee convergence for all trait combinations and data sets of interest in practice. Research is therefore needed into computational methods that could be used to solve these equations efficiently and reliably for all potential data sets of interest, and possibly for alternative sets of constraints that may be more effective than the constraints of MACE*. For example, there may be better constraints to account not only for genetic trends but also for selected base generation populations.

4.5. Conclusions

Modifying the implied constraints on genetic group solutions in the MACE* strategies was effective in eliminating or reducing large biases in country comparisons, and as a result significantly reduced ERP for genetic comparisons that included bulls from different countries. The benefits of using the modified constraints were largest on the evaluation scales of exporting countries, where bulls from importing countries were heavily influenced by the genetic group solutions.

The rankings among alternative MACE* strategies, for ERP of different groups of bulls and countries, were similar to the corresponding rankings among traditional MACE strategies. Each MACE* strategy, relative to the corresponding traditional MACE strategy, had consistently smaller ERP for foreign, all and top bulls, and similar ERP for local and

imported bulls, for both the unselected and selected base population simulations. The ERP with any of the RS* or MT* strategies, relative to GAM, were consistently smaller for foreign, all and top bulls, but slightly larger for local and imported bulls.

The average true genetic merits of top bulls identified by any of the MACE* strategies were similar to the corresponding averages for GAM and the traditional MACE strategies. Differences in top bull true merits among strategies were small, due to high proportions of selected bulls in common among the strategies.

5. OVERALL SUMMARY AND RECOMMENDATIONS

Considering the traditional genetic evaluation strategies, ERP for each category of bulls studied were lowest for GAM and highest for the CNV strategies, when base populations were unselected. The reductions in ERP for MACE relative to CNV strategies, however, were approximately 90-100% of the corresponding differences for GAM.

Country comparisons were biased, favouring importing country bulls on the evaluation scales of exporting countries, with all of the traditional genetic evaluation strategies, again when base populations were unselected. The biases for the MACE strategies were attributed to the effects of missing pedigree information because only sire information was used with MACE. In contrast, GAM made use of both sire and dam pedigree information, tracing back to the unselected base generation for all individuals.

Selection-modified MACE* strategies eliminated ($P > .10$) the country biases that were observed with the traditional MACE strategies when base populations were unselected. The modifications in MACE* were changes to the implied constraints on genetic group solutions in the MACE MME, and accounted for the effects of selection that occurred since the base generation. The ERP were smaller for MACE* than MACE as a direct result of the elimination of country biases. The ERP were smaller for MACE* than GAM for foreign, all ($P < .01$) and top ($P < .10$) bulls, but still higher for MACE* than GAM for local and imported bulls ($P < .01$), again when base populations were unselected.

Violation of the no-selection assumption for base generation animals had the largest effects on GAM. With selected base populations, GAM had lower ERP than all MACE strategies ($P < .01$) for local bulls only, and higher ERP for top bulls ($P < .05$). The

selection-modified MACE* strategies had lower ERP than GAM for foreign, all and top bulls ($P < .01$), with larger advantages over GAM than for unselected base populations.

Reductions in ERP for MACE* relative to MACE strategies, with selected base populations, were due to corresponding reductions in country biases. The country biases on exporting country scales of evaluation were reduced by approximately 50% with MACE* relative to MACE. Additional research is warranted to identify genetic evaluation strategies that can eliminate the remaining biases associated with selected base populations.

The GAM was the traditional strategy most sensitive to the effects of semen exchange on country biases and ERP. The biases and ERP with selected base populations were decreased with increasing levels of semen exchange among countries with all strategies, the largest decreases being observed for GAM. Hence, the GAM had relatively smaller biases and ERP among the strategies, with higher levels of semen exchange. The ERP among GAM and MACE strategies that included multiple traits per country were similar for foreign, all and top bulls ($P > .10$) and lower with GAM ($P < .01$) for local and imported bulls, if levels of semen exchange were high.

The CNV, MACE and MACE* strategies that included all traits consistently had lower ERP than corresponding strategies that allowed only one trait per country. The weighting factors used in the MACE and MACE* strategies generally had small effects on bias and ERP, but would be expected to have larger effects in practice where national data structures and evaluation strategies are more variable than in the present simulation. Regardless of the small effects, use of the theoretically preferred weighting factors generally resulted in lower ERP for the present study.

The most important changes to reduce ERP were;

- 1. switching from CNV to either MACE or GAM strategies,**
- 2. switching from one trait to multiple traits per country, and**
- 3. switching from MACE to MACE* to account for selection.**

For all simulations, true genetic merits of the top 10 bulls (top 1%) selected in each country were generally similar ($P>.05$) for MACE, MACE* and GAM strategies, and significantly lower ($P<.05$) for CNV strategies. Short-term rates of global genetic improvement should therefore be similar using any of the MACE, MACE* or GAM strategies to select sires for international use, under conditions similar to those simulated for the present study. Genetic change is cumulative, however, and small differences in the short-term may become more significant as they accumulate over time. General recommendations would be:

- 1. Strategies that allow multiple traits per country should be preferred over strategies that allow only one trait per country, based on consistently lower ERP with the strategies that allowed multiple-traits per country.**
- 2. Traditional MACE strategies are recommended over CNV strategies for international sire comparisons, based on lower ERP and greater expected rates of genetic improvement.**

3. Multiple-trait traditional MACE strategies are recommended over traditional GAM, based on smaller country biases and ERP of international sire comparisons when pedigree and performance data do not trace back to a global base population of individuals that are unrelated and unselected across all countries.
4. The selection-modified MACE* strategies are recommended over all traditional strategies since country biases and ERP of international sire comparisons were smallest for these strategies, particularly the MACE* strategies that allowed multiple traits per country.
5. Among the MACE* strategies, the repeated single-trait per country strategy RSe* or the multiple-traits per country strategy MTi* are recommended, since they had the most desirable properties. These strategies were simplest computationally and were among the strategies with lowest bias and ERP. Additionally, RSe* and MTi* would account for variability in national data structures and genetic evaluation strategies that are known to exist among countries, but were not simulated in the present study.

The MME used for MACE were modified in MACE* by changing the implied constraints on genetic group solutions to account for selection effects on the group solutions. These modifications were required because pedigrees with the sire model of MACE excluded dam information and were therefore incomplete. Similar modifications should also be considered for national and international animal model systems if sire or dam information is not complete back to an unselected base population. Constraint or model alternatives to MACE* that can account for selected base generation populations

should also be studied, since MACE* was only effective in removing selection biases related to genetic trends since the base generation.

The computing algorithm used to solve the selection-modified MME of MACE* was an iterative algorithm that may not guarantee convergence for all data sets of interest in practice. Therefore, research is recommended on general computing algorithms for selection-modified MME.

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APPENDIX 1: Derivation of Mating Probability Equation for Proven Bulls

Mating probabilities for n individuals sum to one, so are on average equal to $1/n$. Linear decreases in probability with increasing animal rank forces the overall average probability to equal the average of the minimum and maximum probabilities:

$$(PM_1 + PM_n) / 2 = 1 / n$$

We wish to impose a constraint that the maximum probability is twice the minimum, with maximum probability assigned to animal 1:

$$PM_1 = 2 * PM_n$$

Combining these equations leads to:

$$\begin{aligned} PM_1 &= 2 * (2/n - PM_1) \\ &= 4/(3n) \\ &= 2/(3n) \end{aligned}$$

The decrease in probability between any two consecutive animals is the average of the total decrease going from animal 1 to animal n :

$$\begin{aligned} PM_i - PM_{i-1} &= (PM_n - PM_1) / (n-1) = -(2/(3n(n-1))) = \delta \\ PM_i &= PM_1 + (i-1)\delta \\ &= 4/(3n) - (i-1)*(2/(3n(n-1))) \\ &= [4/(3n)] * [1 - (i-1)/(2n-2)] \end{aligned}$$

APPENDIX 2: Effective Independent Daughter Lactation Records

Effective daughter contributions (edc) for each lactation trait are appropriate weighting factors for international evaluation if genetic correlations between lactations are ignored. The edc must be deregressed, however, if genetic correlations between lactations are to be used, as in multiple-trait MACE. The deregression prevents over-weighting the information from countries that contribute lactation-specific evaluations relative to those providing a single evaluation averaged across lactations. Residual correlations can be ignored in the multiple-trait MACE model because they are already accounted for in the edc. The objective is to find weighting factors (m_t) for a multiple-trait model, assuming zero residual correlations and non-zero genetic correlations, that yield equivalent prediction error variances to those from single-trait models using edc.

For trait (e.g. lactation) 't' of T traits in a given country;

Let $r_t = R_{tt}$, $g_t = G_{tt}$, $n_t = \text{edc}_t$, $m_t = \text{a deregressed } n_t$, $B = (\text{diag}(m_t/r_t) + G^{-1})^{-1}$, and $b_t = B_{tt}$.

We wish to find m_t such that $b_t = (n_t/r_t + 1/g_t)^{-1}$

$$\Rightarrow b_t = r_t g_t / (n_t g_t + r_t)$$

$$\Rightarrow n_t = r_t (g_t - b_t) / (g_t b_t)$$

The problem can be solved by iteration, one animal at a time, as follows:

1. $i = 0$
2. $m_t^{(i)} = n_t, \quad t=1, T$
3. Compute $B^{(i)}$
4. $err_t^{(i)} = n_t - r_t(g_t - b_t^{(i)}) / (g_t b_t^{(i)}), \quad t=1, T$
5. $m_t^{(i+1)} = m_t^{(i)} + err_t^{(i)} * relax, \quad t=1, T$
6. $i = i+1$
7. Until $(\max(err_t^{(i-1)}) < threshold)$ goto 3

Convergence was generally reached with fewer than 20 iterations in the present study, with $relax=.5$ and $threshold=.001$.