International Dairy Sire Evaluation Based on Multiple-Trait BLUP Analysis of Daughter Performance Records

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ABSTRACT

Our objective was to estimate variance components and predict sire EBV for milk, fat, and protein yield using a multiple-trait model in which lactation yield in each country was a different trait. Data included first lactation records of 16,145,832 Holstein-sired cows that calved between January 1, 1990 and December 31, 1997 in 243,466 herds in seventeen leading dairy countries. Milk, fat, and protein were analyzed separately using a 17-trait sire model; "traits" refer to measurements of the same biological parameter in different production systems. Our genetic model included effects of herd-year-season of calving, age at calving, milking frequency, and heterosis class (i.e., breed composition). Heritability estimates ranged from 0.24 in Australia (protein) to 0.34 in Israel (milk) and Netherlands (fat). Genetic correlations between countries ranged from 0.77 for Austria-Czech Republic (protein), Estonia-Finland (fat), Estonia-Ireland (milk), Estonia-Israel (milk), and Hungary-New Zealand (fat), to 0.96 for Australia-Ireland (milk), Australia-New Zealand (milk), Belgium-Netherlands (milk), and Belgium-USA (fat). Correlations differed from parameters used currently in international sire evaluations. In particular, genetic correlations were 0.91 – 0.96 between Australia, Ireland, and New Zealand; these countries rely heavily on rotational grazing. Correlations were also 0.91 – 0.96 between Belgium, Canada, Italy, Netherlands, and USA; these countries use intensive management systems. Correlations between these groups of countries were 0.80 – 0.90. The percent of elite bulls selected in common by each pair of countries ranged from 0.42 for Germany-Estonia and Germany-Israel to 0.78 for Belgium-Netherlands.

Introduction

International comparisons of dairy sires rely on methods to combine national EBV that are calculated independently in each participating country. In the past, regression-based conversion equations were developed for each pair of countries using data from foreign bulls with imported semen (Goddard, 1995; Wilmink et al., 1986) or sets of full-sib bulls with offspring in both countries (Mattalia and Bonaiti, 1993). Currently, the multiple-trait across country evaluation (**MACE**) procedure (Schaeffer, 1994) uses national sire EBV from all participating countries simultaneously, and progeny performance in each country is considered as a different trait in a multiple-trait analysis. The International Bull Evaluation Service (**INTERBULL**) has used MACE for routine international dairy sire evaluation since 1994 (Banos and Sigurdsson, 1996).

Lohuis and Dekkers (1998) discussed the concept of border-less genetic evaluations and suggested using individual animal performance records, rather than sire breeding values. Weigel and Rekaya (2000) developed a multiple-trait herd cluster model for international sire evaluation in which herds are grouped across country borders using information about the production conditions in each herd. They applied this model to data from eight countries and five regions of the US. However, many leading dairy countries did not participate, and countries that feature rotational grazing as the management norm were missing. In addition, they used mature equivalent first lactation records that were standardized in a different manner by each participating country, and this introduced an additional source of variation in the analysis.

Our objective was to investigate the possibility of international dairy sire evaluation using individual animal performance records from a large and diverse group of countries and to attempt to control as much variation as possible from data collection through prediction of sire breeding values.

Materials and Methods

Data included test-day observations of first lactation cows in Australia, Austria, Belgium, Canada, Switzerland, Czech Republic, Germany, Estonia, Finland, Hungary, Ireland, Israel, Italy, Netherlands, New Zealand, United States, and South Africa. Data included cows with first calving from January 1, 1994 to December 31, 1997 in Austria, Switzerland, and Estonia; from January 1, 1993 to December 31, 1997 in Ireland; from January 1, 1991 to December 31, 1997 in Czech Republic, and from January 1, 1990 to December 31, 1997 in all other countries. All cows sired by Holstein AI bulls that were present in the INTERBULL pedigree file were included. Monthly milk weights were available for nearly all cows, except those from New Zealand, where bimonthly testing is the norm. Although several countries had a significant percentage of cows on alternate AM/PM testing plans, the vast majority of data were from traditional plans in which all milkings were measured. Cows that were > 90 d postpartum at the first reported test date were excluded, as were cows with only one reported test during the lactation. Additional edits required a minimum of five progeny per sire. After editing, records from 16,145,832 cows in 243,466 herds remained for analysis.

Test-day observations for milk, fat, and protein were combined into lactation yields using Wood's function (e.g., Rekaya et al., 1996). Reference curves were developed by applying this function to the group of cows in each region by production level class that had completed lactation records. Resulting extension factors were used to compute lactation yields from cows in these classes with incomplete records. Because very few cows in rotational grazing systems completed a 305 d lactation, shorter lactation lengths were applied to some countries; lactation records were standardized to 270 d for New Zealand, 290 d for Australia, Ireland, and South Africa, and 305 d for other countries.

Genetic and residual (co)variances and sire breeding values were estimated using a Bayesian implementation of a multiple-trait sire model with relationships via Gibbs sampling. Traits were defined according to country borders. Separate analyses were carried out for milk, fat, and protein yield. Weakly informative normal prior distributions were assumed for systematic effects, and bounded uniform prior distributions were assumed for (co)variance components. For sire breeding values, a multivariate normal prior distribution was used. Genetic relationships between sires with progeny in different countries permitted estimation of a genetic covariance matrix of order 17. However, no individual animals had observations in more than one country, so residual covariances between traits (countries) did not exist. The following model was used for estimation of (co)variance components and prediction of sire breeding values; all factors were nested within country:

$$y_{ijklmn} = \text{herd-year-season}_i + \text{age}_j + \text{frequency}_k + \text{heterosis}_l + \text{sire}_m + \text{error}_{ijklmn}$$

where:

y_{ijklmn} = first lactation milk, fat, or protein yield,
$\text{herd-year-season}_i$ = herd, year, and season of calving (3-month seasons),
age_j = age at calving (groups based on age in months),
frequency_k = number of times milked per day,
heterosis_l = heterosis (breed composition) class,
sire_m = sire of cow, and
error_{ijklmn} = random error.

Because of small herd-year-season classes in some countries, contemporary groups were formed using expanding year-season classes and fuzzy logic (Rekaya et al., 1999). For herd-year-season classes with ≥ 5 observations, all cows calving within this time period received full membership in the corresponding contemporary group. If < 5 observations were found within a herd-year-season class, membership was extended to adjacent groups, and membership values depended on the calving date within a particular season. If < 5 observations existed within a herd-year-season class after expansion, membership was extended into adjacent seasons again, and a particular cow could have nonzero membership in up to five classes. Heterosis classes were formed by tracing three-generation pedigrees, calculating breed composition based on ancestor breed codes, and grouping animals accordingly. The number of heterosis classes varied from one to seven for each country. Most cows were 100% Holstein, but a significant number of cows in certain countries carried either 25% or 50% Jersey, Brown Swiss, Simmental, or Ayrshire genes. Lastly, genetic groups were included for animals with unknown parentage based on time, sex, and country of origin.

Results and Discussion

A summary of the data is in Table 1. Size of the national dairy populations, as measured by the number of first lactation cows from Holstein AI sires, varied substantially, from fewer than 14,000 cows in Austria to more than 4.7 million in the US. Herd size also varied dramatically, from slightly more than two first parity cows per herd-year in Finland to more than 60 in Hungary. These differences in herd size and population size create several problems in sire evaluation. Most obvious is the extreme difficulty in creating herd-year-season classes of sufficient size in some countries. Various strategies, such as random herd-year-seasons or fuzzy logic, can be attempted, but information regarding the management conditions in a given herd at a given point in time is lacking no matter what approach is taken. Furthermore, in a multiple-trait analysis, adding a small country (e.g., with 10,000 cows) could increase the computational burden as much as adding a large country (e.g., with 5 million cows), even though little additional information is gained.

Table 2 shows the number of bulls in common for each pair of countries. This ranged from 0 for Australia – Estonia and Switzerland – Estonia to 1357 for Canada-USA. Information is extremely limiting for certain pairs of countries and extremely plentiful for others. Although 21 pairs of countries shared ≥ 300 common bulls, there were 20 pairs of countries that shared < 10 common bulls. Bulls within the latter group of country pairs may share other genetic relationships, e.g., as half-sibs, cousins, etc., but the lack of direct genetic ties provided by common bulls leads to imprecise genetic parameters and sire breeding values.

Table 3 shows estimated heritability for milk yield in each country, estimated genetic correlations for milk yield between each pair of countries, and posterior standard deviations (**SD**) corresponding to the estimated correlations. Heritability estimates ranged from 0.25 in Finland to 0.34 in Israel. Some estimates differed from those currently used in national genetic evaluations within these countries, because our estimates were based on first lactation Holsteins using a sire model, and within-country parameters often come from animal models, test-day models, or multi-breed models. Genetic correlations ranged from 0.77 for Estonia-Ireland and Estonia-Israel to 0.96 for Australia-New Zealand, Belgium-Netherlands, and Ireland-New Zealand. In general, genetic correlations between countries with a high genetic level, intensive management, and adequate genetic links were similar to correlations calculated from sire breeding values that are used by INTERBULL for routine international sire evaluations. Estimated genetic correlations between countries with weak genetic ties tended to be lower than parameters currently used by INTERBULL, but it is important to note that the latter are often “inferred” based on similar pairs of countries with adequate ties, rather than estimated from the data. Lastly, estimated correlations between Ireland and both Australia and New Zealand were much higher than values currently used by INTERBULL. Posterior SD ranged from 0.01 for Canada-USA (1357 common bulls) to 0.06 for Estonia-Israel (1 common bull).

Table 4 shows estimated heritability for fat yield in each country, estimated genetic correlations for fat yield between each pair of countries, and corresponding posterior SD. Heritability was lowest (0.26) in Estonia and Finland and highest (0.34) in the Netherlands. Estimated genetic correlations ranged from 0.77 for Estonia-Finland and Hungary-New Zealand to 0.96 for Belgium-USA. In general, correlation patterns were similar to those observed for milk yield. Posterior SD ranged from 0.01 for Canada-USA to 0.06 for Australia-Estonia (0 common bulls), Australia-Israel (18 common bulls), Finland-Israel (6 common bulls), and Israel-Italy (34 common bulls).

Table 5 shows estimated heritability for protein yield in each country, estimated genetic correlations for protein yield between each pair of countries, and corresponding posterior SD. Estimated heritability was lowest (0.24) in Australia and highest (0.33) in the Netherlands. Genetic correlations ranged from 0.77 for Austria-Czech Republic to 0.95 for Belgium-USA. Posterior SD were slightly larger for protein, because some cows were missing data for this trait. The SD ranged from 0.02 for Belgium-Canada (247 common bulls) and Belgium-Germany (382 common bulls) to 0.07 for Australia-Estonia, Estonia-South Africa (1 common bull), Finland-Israel, Israel-Italy, and Italy-Switzerland (70 common bulls).

Estimated genetic correlation parameters are of great practical importance, because they determine the relative weight given to information from each country when calculating the international sire breeding values on various country scales. Correlation estimates differed substantially from those currently used in international sire evaluations. In particular, correlations were ≥ 0.91 between countries that rely heavily on rotational grazing, such as Australia, Ireland, and New Zealand. Correlations were also ≥ 0.91 between Belgium, Canada, Italy, Netherlands, and USA, all countries that feature high milk production in intensively managed herds. Correlations between the intensively managed countries and rotational grazing countries ranged from 0.80 - 0.90. Correlations between countries that shared few common bulls, such as Estonia, Finland, and Israel were generally low, ranging from 0.77 to 0.81. These estimates may reflect differences between production systems in these countries, or they may simply reflect a lack of information due to poor genetic ties between countries. Lack of genetic ties is a problem with respect to the precision of the estimated genetic correlations. A posterior SD of 0.07 may not seem large, but a value of this magnitude leads to an extremely large highest posterior density region. For example, the estimated genetic correlation between Finland and Israel for protein yield was 0.78 with an approximate 95% highest posterior density region of 0.64 to 0.92. Given the importance of the genetic correlations parameters in international sire evaluations, it is unacceptable to have such imprecise estimates. Options such as incorporating informative prior distributions for covariance matrices or reducing the number of traits should be considered.

Table 6 shows the percentage of elite bulls (top 1% or top 0.25% for milk yield) selected in common by each pair of countries using estimated breeding values from the multiple-trait analysis. When selecting the top 1%, the percentage of bulls in common ranged from 0.42 for Germany-Estonia and Germany-Israel to 0.78 for Belgium-Netherlands. When selecting the top 0.25%, the percentage in common ranged from 0.39 for Australia – Italy, Switzerland – Estonia, and Switzerland – Italy to 0.78 for Belgium – Finland. Among rotational grazing countries such as Australia, Ireland, and New Zealand, the proportion in common ranged from 0.60 to 0.76. Among intensively managed countries, such as Canada, Netherlands, Italy, and USA, the proportion in common ranged from 0.49 to 0.71. The proportion of bulls selected in common between these two groups of countries ranged from 0.39 to 0.65.

Conclusions

It appears that international genetic evaluation of dairy sires using a multiple-trait sire model, or perhaps a multiple-trait sire-maternal grandsire model, is technically feasible. However, computational limitations will require that such a model will be less precise than the models used for national breeding value estimation in several leading countries. For example, the first lactation sire model described herein does not account for preferential mating, nor does it consider data from repeated lactations. In the future, advancements in computing power will make an international animal model feasible, but by then many countries will be using test-day models for national breeding value estimation. In addition, several issues must be resolved before the strategy discussed in this paper can be adopted in practice. First, the number of common bulls between many pairs of countries is extremely small, and estimated genetic correlations between these pairs of countries are imprecise. Most countries continue to import dairy sire semen, but it will take many years to develop adequate links between some pairs of countries. Furthermore, estimated correlations between pairs of countries that share few common bulls tend to be low, and it is not clear whether these estimates reflect real differences in herd management or simply a lack of information. Regardless of whether one chooses to pursue direct analysis of progeny lactation data or re-analysis of national sire breeding values using MACE, more precise estimates of genetic correlations are needed. Second, the computational burden increases as the number of participating countries increases. The addition of small countries can be especially problematic, because the amount of new information provided by these countries may not be enough to offset the added computational burden. Nonetheless, it may be politically unacceptable for an organization such as INTERBULL to decline data from such countries. In practice, it is likely that the number of unique production environments is much smaller than the number of participating countries. Based on this study, it appears that one might logically group rotational grazing countries into one trait and intensively managed countries into a second trait. However, it is not clear how to handle countries that share few genetic ties with other countries in the analysis. Third, differences in production systems between and within countries are substantial, and definition of a standard lactation length for all systems is not straightforward. Test-day models offer greater flexibility, at least for investigating this problem with a subset of data, but use of a test-day model for the full data set is not possible at present. In addition, it may be inappropriate to use the same set of fixed effects in each country, and therefore it may be necessary to use different models for different countries. Future research will focus on testing the goodness of fit of the multiple-trait model, relative to a single-trait model (ignoring genotype by environment interaction) and a multiple-trait herd cluster model (where traits are defined across country borders according to production systems). In addition, an international test-day model will be considered with a subset of data due to differences in lactation length and milk testing programs between countries. Multiple lactations per cow should also be considered, because most countries consider later parities, but this will increase the computational burden. Lastly, development of methods to incorporate informative priors for (co)variance matrices should be considered, and management factors that cause genotype by environment interactions between herds should be identified. Results of this study can enhance our understanding of the possibilities and limitations in international sire evaluations, and the resulting parameter estimates could be used within the present MACE system, if desired.

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Table 1. Summary of data used in the present study.

Country/Region	No. Herds	No. Cows
Australia	9651	934,931
Austria	2209	13,991
Belgium	3028	75,656
Canada	14,447	1,062,664
Switzerland	2727	49,010
Czech Republic	14,897	208,338
Germany	65,802	3,424,192
Estonia	1481	25,496
Finland	14,176	137,067
Hungary	1354	440,624
Ireland	6453	173,215
Israel	1103	223,416
Italy	17,584	1,470,053
Netherlands	26,340	1,510,595
New Zealand	18,450	1,559,093
United States	42,478	4,701,528
South Africa	1286	135,963
Total	243,466	16,145,832

Table 2. Number of common bulls that had progeny in each pair of countries. Country codes are as follows: AUS = Australia, AUT = Austria, BEL = Belgium, CAN = Canada, CHE = Switzerland, CSK = Czech Republic, DEU = Germany, EST = Estonia, FIN = Finland, HUN = Hungary, IRL = Ireland, ISR = Israel, ITA = Italy, NLD = Netherlands, NZL = New Zealand, USA = United States, ZAF = South Africa.

	AUS	AUT	BEL	CAN	CHE	CSK	DEU	EST	FIN	HUN	IRL	ISR	ITA	NLD	NZL	USA	ZAF
AUS		32	166	502	53	83	217	0	9	171	193	18	214	200	474	529	149
AUT			52	45	33	77	175	2	4	51	48	2	69	79	30	53	30
BEL				247	58	227	382	4	16	189	242	24	285	412	147	392	151
CAN					83	125	341	1	14	329	201	26	372	293	317	1357	249
CHE						43	76	0	6	49	61	4	70	65	48	86	43
CSK							492	7	15	141	212	15	173	254	98	185	86
DEU								16	23	267	266	25	494	590	189	529	191
EST									2	2	5	1	6	14	2	2	1
FIN										23	17	6	19	18	10	24	11
HUN											150	56	294	240	163	492	175
IRL												19	202	299	182	227	116
ISR													34	35	25	47	14
ITA														405	190	647	182
NLD															197	509	171
NZL																362	126
USA																	379
ZAF																	

Table 3. Estimated genetic correlations (above diagonal), heritabilities (on diagonal), and posterior standard deviations (below diagonal) between countries for milk yield. Country codes are as follows: AUS = Australia, AUT = Austria, BEL = Belgium, CAN = Canada, CHE = Switzerland, CSK = Czech Republic, DEU = Germany, EST = Estonia, FIN = Finland, HUN = Hungary, IRL = Ireland, ISR = Israel, ITA = Italy, NLD = Netherlands, NZL = New Zealand, USA = United States, ZAF = South Africa.

	AUS	AUT	BEL	CAN	CHE	CSK	DEU	EST	FIN	HUN	IRL	ISR	ITA	NLD	NZL	USA	ZAF
AUS	**0.30**	0.84	0.85	0.82	0.81	0.87	0.83	0.83	0.87	0.79	0.94	0.81	0.84	0.84	0.96	0.86	0.84
AUT	0.04	**0.26**	0.86	0.89	0.89	0.82	0.88	0.79	0.86	0.78	0.80	0.87	0.88	0.88	0.82	0.88	0.81
BEL	0.03	0.03	**0.31**	0.94	0.91	0.81	0.90	0.80	0.84	0.83	0.82	0.89	0.92	0.96	0.86	0.95	0.84
CAN	0.03	0.02	0.02	**0.33**	0.91	0.86	0.93	0.82	0.89	0.86	0.83	0.84	0.94	0.93	0.89	0.95	0.88
CHE	0.04	0.03	0.03	0.03	**0.27**	0.82	0.91	0.79	0.84	0.82	0.80	0.79	0.91	0.90	0.86	0.93	0.84
CSK	0.03	0.03	0.02	0.03	0.04	**0.32**	0.86	0.81	0.83	0.80	0.82	0.85	0.84	0.87	0.82	0.86	0.83
DEU	0.03	0.02	0.02	0.02	0.03	0.01	**0.32**	0.80	0.87	0.81	0.85	0.83	0.93	0.92	0.91	0.93	0.88
EST	0.05	0.04	0.04	0.04	0.05	0.04	0.04	**0.26**	0.78	0.81	0.77	0.77	0.80	0.82	0.78	0.81	0.81
FIN	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.05	**0.25**	0.79	0.87	0.79	0.86	0.85	0.83	0.88	0.82
HUN	0.04	0.03	0.04	0.02	0.03	0.03	0.03	0.04	0.04	**0.26**	0.78	0.82	0.83	0.85	0.78	0.85	0.78
IRL	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.04	0.03	0.03	**0.33**	0.83	0.82	0.82	0.96	0.83	0.82
ISR	0.05	0.05	0.04	0.03	0.04	0.04	0.03	0.06	0.05	0.03	0.04	**0.34**	0.82	0.83	0.82	0.87	0.78
ITA	0.03	0.03	0.04	0.04	0.04	0.03	0.03	0.05	0.05	0.04	0.04	0.05	**0.32**	0.92	0.85	0.94	0.83
NLD	0.04	0.02	0.02	0.03	0.03	0.02	0.02	0.04	0.04	0.03	0.02	0.04	0.03	**0.33**	0.87	0.94	0.86
NZL	0.02	0.02	0.03	0.02	0.03	0.03	0.03	0.05	0.04	0.03	0.04	0.04	0.03	0.03	**0.32**	0.88	0.90
USA	0.03	0.02	0.02	0.01	0.03	0.03	0.02	0.04	0.04	0.02	0.03	0.03	0.04	0.02	0.02	**0.29**	0.89
ZAF	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.05	0.04	0.04	0.03	0.04	0.04	0.03	0.03	0.03	**0.32**

Table 4. Estimated genetic correlations (above diagonal), heritabilities (on diagonal), and posterior standard deviations (below diagonal) between countries for fat yield. Country codes are as follows: AUS = Australia, AUT = Austria, BEL = Belgium, CAN = Canada, CHE = Switzerland, CSK = Czech Republic, DEU = Germany, EST = Estonia, FIN = Finland, HUN = Hungary, IRL = Ireland, ISR = Israel, ITA = Italy, NLD = Netherlands, NZL = New Zealand, USA = United States, ZAF = South Africa.

	AUS	AUT	BEL	CAN	CHE	CSK	DEU	EST	FIN	HUN	IRL	ISR	ITA	NLD	NZL	USA	ZAF
AUS	**0.29**	0.83	0.84	0.83	0.78	0.85	0.80	0.84	0.87	0.81	0.92	0.80	0.86	0.87	0.95	0.85	0.79
AUT	0.03	**0.28**	0.88	0.86	0.90	0.79	0.86	0.81	0.85	0.80	0.81	0.84	0.85	0.89	0.82	0.87	0.83
BEL	0.04	0.02	**0.29**	0.93	0.90	0.82	0.91	0.82	0.86	0.83	0.82	0.87	0.91	0.95	0.87	0.96	0.85
CAN	0.04	0.02	0.02	**0.30**	0.92	0.87	0.91	0.80	0.90	0.85	0.84	0.80	0.92	0.95	0.88	0.94	0.89
CHE	0.04	0.04	0.03	0.02	**0.29**	0.84	0.93	0.81	0.86	0.81	0.82	0.81	0.91	0.92	0.90	0.91	0.85
CSK	0.03	0.03	0.02	0.03	0.03	**0.33**	0.82	0.80	0.84	0.83	0.81	0.85	0.83	0.87	0.83	0.85	0.84
DEU	0.03	0.02	0.02	0.01	0.02	0.02	**0.30**	0.81	0.86	0.84	0.84	0.81	0.91	0.93	0.90	0.93	0.85
EST	0.06	0.03	0.04	0.04	0.05	0.05	0.03	**0.26**	0.77	0.81	0.79	0.79	0.78	0.83	0.81	0.84	0.83
FIN	0.05	0.04	0.03	0.04	0.04	0.04	0.04	0.04	**0.26**	0.81	0.84	0.80	0.85	0.84	0.82	0.89	0.84
HUN	0.04	0.02	0.04	0.02	0.03	0.03	0.03	0.03	0.05	**0.28**	0.80	0.80	0.79	0.82	0.77	0.87	0.82
IRL	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.05	0.03	0.03	**0.30**	0.85	0.81	0.81	0.95	0.85	0.83
ISR	0.06	0.04	0.04	0.03	0.04	0.03	0.03	0.05	0.06	0.03	0.03	**0.32**	0.84	0.86	0.83	0.83	0.81
ITA	0.05	0.04	0.03	0.03	0.05	0.03	0.03	0.04	0.04	0.03	0.03	0.06	**0.30**	0.92	0.82	0.93	0.82
NLD	0.04	0.04	0.03	0.02	0.02	0.02	0.02	0.03	0.04	0.02	0.02	0.04	0.03	**0.34**	0.89	0.92	0.88
NZL	0.03	0.03	0.04	0.02	0.02	0.03	0.02	0.05	0.04	0.02	0.03	0.04	0.03	0.03	**0.33**	0.85	0.89
USA	0.03	0.02	0.03	0.01	0.02	0.03	0.02	0.04	0.03	0.03	0.03	0.04	0.04	0.02	0.02	**0.27**	0.90
ZAF	0.04	0.03	0.03	0.05	0.04	0.03	0.03	0.05	0.05	0.04	0.03	0.04	0.03	0.04	0.03	0.03	**0.29**

Table 5. Estimated genetic correlations (above diagonal), heritabilities (on diagonal), and posterior standard deviations (below diagonal) between countries for protein yield. Country codes are as follows: AUS = Australia, AUT = Austria, BEL = Belgium, CAN = Canada, CHE = Switzerland, CSK = Czech Republic, DEU = Germany, EST = Estonia, FIN = Finland, HUN = Hungary, IRL = Ireland, ISR = Israel, ITA = Italy, NLD = Netherlands, NZL = New Zealand, USA = United States, ZAF = South Africa.

	AUS	AUT	BEL	CAN	CHE	CSK	DEU	EST	FIN	HUN	IRL	ISR	ITA	NLD	NZL	USA	ZAF
AUS	**0.24**	0.81	0.81	0.82	0.81	0.87	0.82	0.83	0.89	0.85	0.91	0.83	0.88	0.86	0.94	0.85	0.82
AUT	0.05	**0.26**	0.84	0.85	0.88	0.77	0.87	0.83	0.84	0.81	0.82	0.82	0.87	0.91	0.84	0.88	0.83
BEL	0.05	0.03	**0.26**	0.94	0.89	0.83	0.90	0.83	0.83	0.84	0.80	0.85	0.92	0.93	0.88	0.95	0.86
CAN	0.06	0.03	0.02	**0.30**	0.92	0.89	0.92	0.83	0.92	0.86	0.86	0.82	0.91	0.93	0.90	0.92	0.90
CHE	0.05	0.05	0.04	0.02	**0.28**	0.82	0.93	0.84	0.88	0.85	0.87	0.80	0.92	0.91	0.91	0.92	0.88
CSK	0.04	0.03	0.03	0.04	0.04	**0.28**	0.84	0.82	0.85	0.81	0.80	0.83	0.83	0.90	0.85	0.88	0.81
DEU	0.04	0.04	0.02	0.03	0.03	0.04	**0.32**	0.84	0.89	0.87	0.83	0.82	0.92	0.93	0.91	0.94	0.87
EST	0.07	0.04	0.05	0.04	0.05	0.06	0.05	**0.26**	0.80	0.83	0.81	0.81	0.79	0.81	0.84	0.85	0.87
FIN	0.06	0.05	0.04	0.05	0.05	0.05	0.04	0.05	**0.27**	0.80	0.86	0.78	0.86	0.85	0.81	0.87	0.83
HUN	0.06	0.03	0.05	0.04	0.04	0.05	0.04	0.04	0.06	**0.30**	0.82	0.80	0.82	0.84	0.78	0.87	0.86
IRL	0.05	0.05	0.03	0.04	0.04	0.05	0.04	0.05	0.04	0.05	**0.29**	0.85	0.83	0.83	0.94	0.86	0.84
ISR	0.06	0.04	0.04	0.04	0.06	0.03	0.04	0.06	0.07	0.04	0.04	**0.27**	0.85	0.87	0.84	0.86	0.79
ITA	0.06	0.04	0.04	0.04	0.07	0.04	0.04	0.06	0.05	0.05	0.04	0.07	**0.28**	0.92	0.85	0.92	0.85
NLD	0.05	0.05	0.04	0.03	0.03	0.03	0.03	0.04	0.04	0.03	0.03	0.05	0.03	**0.33**	0.88	0.93	0.89
NZL	0.05	0.04	0.04	0.04	0.04	0.04	0.03	0.06	0.05	0.03	0.04	0.05	0.04	0.04	**0.27**	0.87	0.90
USA	0.04	0.03	0.05	0.03	0.03	0.05	0.03	0.05	0.04	0.04	0.03	0.05	0.05	0.03	0.03	**0.26**	0.90
ZAF	0.06	0.04	0.05	0.05	0.04	0.04	0.04	0.07	0.05	0.05	0.03	0.06	0.04	0.05	0.05	0.04	**0.31**

Table 6. Proportion of selected bulls in common when selecting the top 1% (N = 665, above diagonal) and the top 0.25% (N = 166, below diagonal) of AI sires for milk yield on the scale of each pair of countries. Country codes are as follows: AUS = Australia, AUT = Austria, BEL = Belgium, CAN = Canada, CHE = Switzerland, CSK = Czech Republic, DEU = Germany, EST = Estonia, FIN = Finland, HUN = Hungary, IRL = Ireland, ISR = Israel, ITA = Italy, NLD = Netherlands, NZL = New Zealand, USA = United States, ZAF = South Africa.

	AUS	AUT	BEL	CAN	CHE	CSK	DEU	EST	FIN	HUN	IRL	ISR	ITA	NLD	NZL	USA	ZAF
AUS		0.52	0.62	0.61	0.48	0.65	0.57	0.57	0.65	0.57	0.71	0.44	0.48	0.61	0.69	0.49	0.58
AUT	0.53		0.71	0.64	0.53	0.63	0.51	0.64	0.70	0.60	0.66	0.71	0.53	0.61	0.65	0.68	0.62
BEL	0.60	0.66		0.72	0.62	0.68	0.66	0.58	0.76	0.64	0.68	0.63	0.63	0.78	0.74	0.71	0.66
CAN	0.57	0.63	0.71		0.52	0.67	0.72	0.52	0.66	0.69	0.63	0.52	0.54	0.69	0.65	0.71	0.74
CHE	0.40	0.45	0.52	0.46		0.51	0.49	0.46	0.56	0.50	0.51	0.51	0.47	0.57	0.54	0.51	0.48
CSK	0.60	0.64	0.70	0.66	0.45		0.60	0.49	0.66	0.62	0.60	0.52	0.51	0.70	0.68	0.60	0.63
DEU	0.50	0.50	0.62	0.70	0.41	0.58		0.42	0.59	0.58	0.54	0.42	0.50	0.67	0.61	0.61	0.67
EST	0.51	0.62	0.61	0.54	0.39	0.53	0.47		0.62	0.54	0.65	0.68	0.46	0.48	0.59	0.54	0.57
FIN	0.61	0.70	0.78	0.68	0.45	0.68	0.60	0.59		0.61	0.71	0.62	0.56	0.69	0.74	0.62	0.63
HUN	0.49	0.58	0.59	0.60	0.40	0.57	0.48	0.52	0.57		0.59	0.58	0.50	0.64	0.60	0.62	0.65
IRL	0.67	0.67	0.71	0.64	0.45	0.62	0.58	0.62	0.70	0.57		0.62	0.52	0.60	0.76	0.59	0.64
ISR	0.40	0.70	0.61	0.51	0.45	0.51	0.40	0.61	0.57	0.57	0.60		0.50	0.54	0.58	0.58	0.54
ITA	0.39	0.43	0.55	0.49	0.39	0.45	0.42	0.42	0.47	0.42	0.45	0.42		0.56	0.55	0.52	0.51
NLD	0.53	0.57	0.74	0.68	0.52	0.69	0.62	0.50	0.69	0.56	0.60	0.51	0.44		0.69	0.65	0.64
NZL	0.60	0.67	0.73	0.67	0.50	0.70	0.61	0.57	0.75	0.57	0.75	0.57	0.45	0.66		0.61	0.62
USA	0.43	0.58	0.61	0.65	0.45	0.53	0.54	0.52	0.57	0.54	0.54	0.54	0.43	0.59	0.55		0.65
ZAF	0.49	0.58	0.63	0.70	0.44	0.60	0.64	0.61	0.57	0.56	0.61	0.51	0.45	0.60	0.60	0.60	