RANDOM HETEROSIS AND RECOMBINATION LOSS EFFECTS IN A MULTIBREED EVALUATION FOR NORDIC RED DAIRY CATTLE

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INTRODUCTION

Denmark, Finland and Sweden joined their resources to establish one common genetic evaluation for dairy cattle. The milk production evaluation for the red breeds comprises of the Red Danish Cattle (RDM) a synthetic breed, the Finnish Ayrshire (FAY), and the Swedish Red Breed (SRB). Further, Finnish Holstein (FBW) and Finncattle (FIC) are included to increase Finnish contemporary group sizes.

While developing the model (Pedersen *et al.*, 2004) it was found that modeling of heterosis and recombination loss is crucial, because the three populations are linked through crossbred animals. For correct across country evaluation of animals it is vital to obtain the same estimates of heterosis and recombination loss for the same crosses in all countries, even if crossbred information is weak. A further problem may arise when observations are available on crossbred animals only. That is the case when a population is upgraded with a foreign breed. Then, there may exist a co-linearity between the heterozygosity of the crossbred animals and the genetic group of the foreign breed. The aim of this work was to overcome the mentioned obstacles and find a different way in modeling heterosis and recombination loss.

MATERIAL AND METHODS

Data. The pedigree for the joint evaluation included 3.9 million animals. It comprised of 13.1% RDM, 39.6% FAY, 33.5% SRB, 11.7% FBW, 0.5% FIC, and 1.6% foreign animals. Genetic ties between the red breeds of the three countries were mainly established through exchange of semen during the last decade (table 1). The data included 45.8 million records on milk, protein, and fat yield. The type of records differed significantly between the countries (table 2).

Breeding value evaluation model. The reduced rank random regression multiple trait animal model included milk, protein and fat yield. The 1st, 2nd, and 3rd plus later parities, as well as countries were defined as different traits. This lead to a model with 27 traits, which allowed modeling of country-specific effects as well as country-specific heritabilities and variances. The animal genetic effect was modeled *via* a meta-model (Mäntysaari, 2006). A unified trait approach (Mäntysaari, 2002) was applied to include Swedish 305-day observations. Imposing a genetic correlation of unity across countries generated for each animal one unique set of 14 regression coefficients for the additive genetic effects. Heterogeneous variance was accounted for by a method based on the multiplicative mixed model given in Meuwissen *et al.* (1996). The method was modified to iteratively calibrate the country levels until the re-estimates of the genetic variances were approximately the same in each country.

Table 1. Number of animals by breed of sire given for animals of the three main breeds

	Red Danish Cattle		Finnish Ayrshire		Swedish Red Breed	
Breed of the sire	Bulls	Cows	Bulls	Cows	Bulls	Cows
Red Danish Cattle	3,435	443,355	0	2	119	4,732
Finnish Ayrshire	23	406	8,982	1,502,803	445	19,703
Swedish Red Breed	251	17,851	532	17,396	6,544	1,134,556
Norwegian Red Cattle	54	360	199	857	444	8,048
Canadian Ayrshire	0	198	47	1,393	70	5,031
Holstein	233	3,836	13	1,472	3	128
Brown Swiss	1,009	14,804	0	0	0	0

Table 2. Type and structure of milk production records by breeds of the three countries

	Time period	Type of data	Included parities	No. of records
Red Danish Cattle	1990 – 2005	test-day yields	3	5,843,443
Finnish Ayrshire	1988 – 2005	test-day yields	all	29,455,501
Swedish Red Breed	1989 – 2005	305-day yields	3	1,866,941
Finnish Holstein	1988 – 2005	test-day yields	all	8,812,902
Finncattle	1988 – 2005	test-day yields	all	364,946

Modeling heterosis and recombination loss. All breeds with significant gene contributions were accounted. These were for Denmark: RDM, SRB, FAY, Brown Swiss (BSW), Red Holstein (RHL), Norwegian Red Cattle (NRF), Jersey (JER) and beef breeds; for Finland: FAY, SRB, NRF, Canadian Ayrshire (CAY), FBW and FIC; and for Sweden: SRB, FAY, RDM, NRF, CAY, and RHL. The covariables for the expected heterozygosity and for the expected recombination loss were calculated based on a two-locus-model (Dickerson, 1973): $h_{ij}^{k} = p_i^s p_j^d + p_j^s p_i^d$ and $r_{ij}^{k} = (p_i^s + p_i^d)(p_j^s + p_j^d) - h_{ij}^{k}$, where h_{ij}^{k} is the heterozygosity for a crossbred animal *k* of breed *i* and breed *j*; p_i^s and p_j^s are the breed shares in sire *s*; p_i^d and p_j^d are the breed shares in dam *d*; and r_{ij}^{k} is the covariable for recombination loss for the same crossbred animal *k*. For Danish cows, FAY and NRF were combined with SRB, and for Swedish cows, BSW was included into RDM. This yielded 15 different heterosis and recombination loss effects for each country.

Since recombination loss was modeled the same way as heterosis, from here onwards, only the model for heterosis is explained. Given the data and pedigree, it could not be expected to obtain reliable estimates for all 45 heterosis effects. One possibility would be to model one total heterosis effect across all countries. However, it would be a strong assumption that different crosses like RHL×BSW and SRB×FAY would have the same heterosis effect. Alternatively, the following strategy was chosen:

A mean heterosis effect across countries. Because of the different data types all heterozygosity covariables were scaled by 1/100 of the country-specific phenotypic means. For each animal k, all covariables for the different crosses were summed to a total heterozygosity c_{TOT}.

Country-specific random heterosis effects. Additionally, the five most important country-specific heterosis effects were included and regressed to the mean heterosis effect by imposing a variance of 1.0. The chosen variance parameter relates to a standard deviation of the random heterosis effect solutions of 1% of the phenotypic mean and was found to be a good compromise between allowing variation in estimates and regressing unreliable estimates toward the mean estimate. Thus, the six heterosis effects in the breeding value evaluation model were:

Denmark: $c_{TOTtd}\, H_t + c_{RDM\times SRBt}\, h_{1td} + c_{BSW\times SRBt}\, h_{2td} + c_{RDM\times BSWt}\, h_{3td} + c_{RDM\times RHLt}\, h_{4td} + c_{BSW\times RHLt}\, h_{5td}$,
Finland: $c_{TOTtf}\, H_t + c_{FAY\times SRBt}\, h_{1tf} + c_{FAY\times NRFt}\, h_{2tf} + c_{SRB\times NRFt}\, h_{3tf} + c_{FAY\times CAYt}\, h_{4tf} + c_{FAY\times FBWt}\, h_{5tf}$,
Sweden: $c_{TOTts}\, H_t + c_{SRB\times FAYt}\, h_{1ts} + c_{FAY\times NRFt}\, h_{2ts} + c_{SRB\times NRFt}\, h_{3ts} + c_{SRB\times CAYt}\, h_{4ts} + c_{SRB\times RDMt}\, h_{5ts}$,

where H_t is the across country mean heterosis effect for trait t and t is milk, protein, and fat yield of 1st, 2nd, and 3rd parity. Note, covariables were different for each trait because of scaling.

Correlated heterosis effects. Correlations were imposed between same random heterosis effects to avoid that genetic levels between the countries are influenced by the heterosis estimates: between Denmark and Sweden $r_{(h1td,\, h5ts)} = r_{(h2td,\, h5ts)} = 0.95$; and between Sweden and Finland $r_{(h1tf,\, h1ts)} = r_{(h2tf,\, h2ts)} = r_{(h3tf,\, h3ts)} = 0.95$.

In addition to the model with random heterosis and recombination loss (RANDOM), a second model (CONTROL) was tested. The CONTROL model included the same heterosis and recombination loss effects, but all effects were fixed and no restrictions were applied between traits. The models were compared using the Nordic Yield Index. First, breeding values of 1st, 2nd, and 3rd parity were weighted by 0.5, 0.3, and 0.2, respectively and standardized to an index with ten index points correspond to the standard deviation of sire breeding values. Second, indices for milk, protein and fat were weighed by –0.25, 1, 0.25, respectively.

RESULTS AND DISCUSSION

Estimates for heterosis and recombination loss were in a reasonable interval when applying the RANDOM model. The largest estimate for heterosis was 6.7% of the phenotypic mean for SRB×RDM in Swedish 1st lactation protein, and the largest estimate for recombination loss was –4.9% for FAY×SRB in Finnish 3rd lactation milk. With the CONTROL model the largest heterosis estimate of 11.9% was found for RDM×RHL in 3rd lactation milk. The corresponding estimate from the RANDOM model was 4.5%. The largest recombination loss effect with the CONTROL model was –16.7 for NRF×SRB in Finnish 2nd lactation milk, whereas with the RANDOM model it was –4.7%.

Estimates for the correlated heterosis and recombination loss effects were similar across countries with model RANDOM (table 3). Overall, Danish estimates increased whereas Finnish estimates decreased compared with the estimates from the CONTROL. As a consequence, genetic level increased for Denmark and decreased for Finland. This affected the ranking of top animals. The correlation between the ranks from both evaluations was 0.91 for the best 100 bulls and 0.89 for the best 1000 cows. Indices of top bulls changed between -1.5 and +1.5 index points with a tendency that the estimated breeding values of Danish bulls increased and those of Finnish bulls decreased.

Table 3. Estimates for heterosis and recombination loss for 1st parity protein yield in % of phenotypic mean (Denmark 0.73kg, Sweden 237kg, and Finland 0.70kg). Effects were random and correlated across countries (RANDOM) or effects were fixed (CONTROL)

	RANDOM			CONTROL		
Crosses	Denmark	Sweden	Finland	Denmark	Sweden	Finland
Estimates for heterosis						
RDM×SRB	6.2	6.7		6.1	7.4	
BSW×SRB	6.4	6.7		8.9	7.4	
FAY×SRB		2.3	2.4		2.6	3.3
FAY×NRF		0.7	0.8		8.0	-1.0
SRB×NRF		2.8	2.7		6.0	5.3
Estimates for recombination loss						
RDM×SRB	-2.3	-2.4		-1.8	-1.9	
BSW×SRB	-2.5	-2.4		-2.8	-1.9	
FAY×SRB		-2.6	-1.9		-1.5	-3.4
FAY×NRF		-4.3	-4.5		-7.5	-2.9
SRB×NRF		-3.1	-3.2		-8.5	-12.7

CONCLUSION

Results shows that modeling heterosis and recombination loss as random can help to overcome the problem of unreliable estimates when crossbred information is weak.

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