EFFECTS OF HETEROSIS ON SIRE EVALUATION AND INTERNATIONAL CONVERSION FACTORS

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Introduction

The primary reason for importing foreign breeding material into an indigenous cattle population is to cause a faster rise in the genetic level than would be possible if the breeding programme was conducted solely on a national basis. New Zealand (NZJ) and American Jerseys (USJ) have been imported into the Danish Jersey (DJ) population, and American Brown Swiss (ABS), Red Holstein (RHF) and Swedish Red and White (SRB) have been imported into the Danish Red (RDM) population. Bulls of these breeds have in recent years been used extensively as bull sires. An unbiased comparison of the breeds is conditional on there being no heterosis or that heterosis is taken into consideration in the statistical models used.

Material and Method

Included in these analyses are cows with 305 day yields in their first lactations and having calved subsequent to the 1 January 1986. Incomplete lactations of more than 45 days were extended to a 305 day equivalent. A total of 199,833 RDM and 222,825 DJ have been included in the analysis.

In Denmark a modified BLUP-Sire model is applied for the calculation of the bulls' breeding values (BVs). In this study, the model was expanded to include breed proportions and the degree of heterozygosity.

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Model:

$$Y_{ijlmnopq} = HY_i + YMR_j + AGE_k + \sum b_m \cdot BREED_m + \sum b_n + HET_n + b \text{ x } mother_o + S_p + e_{ijklmnopq}$$

where

$Y_{ijlmnopq}$	=	305 day yield
HY_i	=	Herd x year
YMR_j	=	Year x month x region
AGE_k	=	Calving age
b_m	=	Breed effect for breed m
$BREED_m$	=	Proportion of breed m
b_n	=	Effect of heterosis for the n'th breed combination
HET_n	=	Heterozygosity for the n'th breed combination
b	=	Regression coefficient on dam's EBV
$mother_o$	=	EBV for dam_o
S_p	=	Sire (random)
$e_{ijlmnopq}$	=	Residual (random)

Precorrection was made for days open.

The model was run separately for RDM and DJ. Furthermore, the model was run for both breeds without the effect of BREED and HET in order to estimate the effect of ignoring the effects of gene immigration in the model.

Breed Proportions and the Degree of Heterozygosity

In this paper heterozygosity is defined as the additional heterozygosity above the proportion that is present on average in the contributing breeds. Heterozygosity is measured as a proportion of the maximum potential heterozygosity.

Table 1 and 2 show the breed proportions and the degree of heterozygosity for first lactation cows, computed per calving year. In both breeds the proportion of foreign genes as well as the degree of heterozygosity have increased between 1986 and 1994.

Table 1. Danish Jersey - Breed proportions and degree of heterozygosity per calving year

Calving year	Breed proportions			Proportion of heterozygosity			
	DJ	NZJ	USJ	DJ x NZJ	DJ x USJ	USJ x NZJ	Aggregate
1986	0.93	0.02	0.04	0.04	0.08	0.002	0.12
1987	0.92	0.03	0.05	0.05	0.09	0.002	0.14
1988	0.92	0.02	0.05	0.04	0.10	0.002	0.14
1989	0.91	0.03	0.06	0.06	0.11	0.003	0.17
1990	0.88	0.05	0.06	0.10	0.11	0.006	0.22
1991	0.87	0.05	0.08	0.09	0.15	0.007	0.25
1992	0.86	0.06	0.08	0.10	0.14	0.009	0.25
1993	0.84	0.05	0.11	0.08	0.20	0.011	0.29
1994	0.83	0.04	0.13	0.07	0.23	0.011	0.31

Table 2. Danish Red - Breed proportions and degree of heterozygosity per calving year

Calving year	Breed proportions				Proportion of heterozygosity						
	RDM	ABS	RHF	SRB	RDM x ABS	RDM x RHF	RDM x SRB	ABS x RHF	ABS x SRB	RHF x SRB	Aggregate
1986	0.83	0.15	0.02	0.000	0.29	0.03	0.000	0.005	0.000	0.000	0.33
1987	0.80	0.17	0.03	0.002	0.30	0.05	0.004	0.007	0.000	0.000	0.36
1988	0.77	0.19	0.04	0.003	0.32	0.06	0.005	0.010	0.000	0.000	0.40
1989	0.75	0.22	0.03	0.001	0.36	0.04	0.001	0.011	0.000	0.000	0.41
1990	0.70	0.26	0.03	0.005	0.39	0.06	0.008	0.016	0.001	0.001	0.48
1991	0.66	0.30	0.03	0.010	0.42	0.04	0.014	0.019	0.005	0.000	0.50
1992	0.64	0.32	0.03	0.005	0.43	0.04	0.007	0.021	0.003	0.000	0.50
1993	0.61	0.34	0.04	0.011	0.43	0.05	0.016	0.028	0.006	0.000	0.53
1994	0.58	0.35	0.06	0.011	0.42	0.08	0.014	0.036	0.008	0.001	0.56

Heterosis Estimates

The heterosis estimates for milk, fat and protein yield as well as the standard error for protein are shown in Table 3. Standard errors for milk and fat are not shown, as standard errors are calculated seperately.

The estimates of heterosis effects agree well with previous Danish investigations (Jensen, 1992; Christensen and Pedersen, 1988) and with an analysis by Metzger et. al. (1994), who found heterosis estimates between DJ and USJ of 153 kg milk, 7.4 kg fat and 6.4 kg protein.

Table 3. *Heterosis estimates for yield traits*

Jersey				
Breed	*Milk, kg*	*Fat, kg*	*Protein, kg*	*s.e., protein, kg*
DJ x USJ	160	8.5	5.2	1.2
DJ x NZJ	172	15.0	9.2	2.8
NZJ x USJ	150	14.4	6.5	3.8
Danish Red				
Breed	*Milk, kg*	*Fat, kg*	*Protein,kg*	*s.e., protein, kg*
RDM x ABS	421	16.4	14.7	0.9
RDM x RHF	431	20.4	15.8	4.0
RDM x SRB	277	- 1.2	5.6	10.1
ABS x RHF	484	24.9	20.0	4.0
ABS x SRB	356	4.8	11.0	10.6
RHF x SRB	- 248	- 2.0	0.7	15.0

The standard error figures depend very much on the breed combination. Standard errors are lowest for crosses between DJ and USJ and between RDM and ABS, whereas the highest standard errors are found in combinations involving the most recently imported breeds, which are not present in very large numbers. This is especially the case when SRB are involved.

Effect on the Ranking of Bulls

When the genes from a foreign breed of cattle are first imported, the first bulls that are progeny tested will have considerably biased estimated breeding values (EBVs). This bias may be up to twice the heterosis effect. For RDM the EBVs of the first ABS bulls were subject to errors amounting to nearly 2 genetic standard deviation units.

Not only foreign bulls will be ranked incorrectly. If bulls from a different breed are used as bull sires, the heterosis effect will result in progeny tested bulls being incorrectly ranked. Table 4 shows the correlation between EBVs when the heterosis effect was taken into account versus when it was not taken into account. The results were calculated per year group of bulls. The bulls belong to the year where the major part of their first batch daughters complete their first 305 day lactation.

Table 4. *Correlation between breeding values for protein, taking into account heterosis and leaving it out of consideration, calculated per year group*

Year Group	Danish Red		Jersey	
	No. of bulls	*Correlation*	*No. of bulls*	*Correlation*
1988	92	0.81	78	0.96
1989	90	0.85	79	0.97
1990	88	0.91	98	0.94
1991	94	0.91	99	0.94
1992	92	0.95	98	0.98
1993	78	0.94	70	0.97
1994	40	0.96	43	0.99

When heterosis is ignored in the prediction of the breeding values of the bulls, the ranking of the bulls will change with the altered breed proportion in the dams. Table 5 illustrates the possible change in estimated genetic merit of two bulls, assuming they actually were equal in additive genetic value but one bull was 75% ABS and 25% RDM, whereas the other was 100% RDM. If the bulls were progeny tested in 1987, the daughters of bull 1 would yield approx. 9 kg more protein than those of bull 2. If the same two bulls were tested in the year 2000, the daughters of bull 2 should yield approx. 2 kg more protein than those of bull 1. In the course of the intervening 13 years, the alteration in EBVs would amount to approx. 20 kg protein.

Table 5. The effect of leaving heterosis out of the model on the genetic evaluation of two hypothetical bulls

Assumptions:	Heterosis : 15 kg protein Bull 1 : 25% RDM, 75% ABK Bull 2 : 100% RDM The bulls are equal in additive genetic value. Breed proportions in dams: Calving year 1987 90% RDM 10% ABK 1994 75% RDM 25% ABK 1997 60% RDM 40% ABK 2000 40% RDM 60% ABK					
Progeny	**Bull 1**		**Bull 2**		**Bull 1 - Bull 2**	
Calving year	*Heterozygosity %*	*Effect Protein kg*	*Heterozygosity %*	*Effect Protein kg*	*Heterozygosity %*	*Effect Protein kg*
1987	70	10.5	10	1.5	60	9.0
1994	63	9.4	25	3.8	38	5.7
1997	55	8.3	40	6.0	15	2.3
2000	45	6.8	60	9.0	- 15	- 2.2

Effect on the Estimates of Genetic Trend

For protein yield in DJ and RDM, the effect on estimates of genetic trend of including heterosis in the calculation of BVs was investigated. In DJ no changes were found. However, over the last 6 years the RDM genetic trend was overestimated by approx. 5 kg protein - when heterosis was ignored. The effect on the genetic trends for milk and fat has not been investigated.

Due to a changed breed propotion by year in the dams the degree of heterozygosity will be less in second batch daughters than in first batch daughters, and compared to bulls of the same age with no second batch daughters, this will result in a decreasing DYD-value and EBV by year, cf. Table 5. It should be investigated whether the methods suggested by "Interbull" (1994) will allow the detection of an overestimated genetic trend, when it is caused by heterosis. Estimates of genetic trend will only be unbiased if heterosis is taken into account in the calculation of EBVs.

Effect on Conversion Formulas

In Denmark EBVs are published as relative figures with a genetic base equal to 100. The average overestimation of genetic merit caused by neglecting heterosis of USJ and ABS bulls at present amounts to 3 - 4 percentage units. The reason why this overestimation is of the same magnitude in spite of different degrees of heterosis is that the progeny tested RDM bulls have 65% genes from ABS, RHF and SRB, whereas DJ has 23% genes from USJ and NZJ. Furthermore, the percentage of foreign genes in dams is high for RDM.

So far official conversion factors have not been calculated for RDM and DJ, because of the low number of bulls which have been progeny tested in both countries.

Applying the Wilmink method for estimating conversion factors on the basis of bulls born after 1975 yielded the a- and b-values in Table 6 (American PTAs (predicted transmitting abilities) converted into kg).

Table 6. Conversion factors between the USA and Denmark

	n	a	b	Correlation
RDM - Protein				
Heterosis considered	16	92	0.70	0.89
Heterosis not considered	16	95	0.65	0.85
DJ				
Heterosis considered				
Milk	12	100	0.037	0.91
Fat	12	84	0.68	0.93
Protein	12	95	0.84	0.92
Heterosis not considered				
Milk	12	104	0.037	0.90
Fat	12	87	0.68	0.93
Protein	12	98	0.84	0.92

As expected the a-values were reduced by approx. 3 units. When taking heterosis for RDM into consideration, the correlation between the Danish EBVs and the American PTAs increased, which among other things is due to the fact that the daughters of the various bulls calved in different years, and different degrees of heterosis have thus come into play, cf. examples shown in Table 5.

With DJ the change over time in the degree of heterozygosity is less pronounced, and correlations between the American PTAs and the Danish EBVs with heterosis included or ignored are therefore of a similar magnitude.

Four DJ bulls have had their PTAs calculated in the USA with a reliability of at least 75%. Table 7 shows the official US PTAs and Danish EBVs.

Table 7. *Official PTAs and EBVs for 4 Danish DJ bulls*

	USA, PTA, kg			Denmark Relative EBVs		
	Milk	Fat	Protein	Milk	Fat	Protein
FYN Aalbaek	44	29	15	90	94	96
FYN Haug	273	53	22	104	113	107
FYN Tved	156	46	14	100	108	101
FYN Index	- 25	36	9	95	111	100
Average				97.3	106.5	101

As Danish genes are not widespread in the USA, PTAs for Danish bulls estimated in America will be strongly influenced by heterosis. If the heterosis estimates were subtracted from the American proofs and if they were then converted into relative Danish EBVs, the result would be as shown in Table 8.

On average - by including the heterosis effect in the calculations of both countries, a better result can be achieved when converting the American PTAs of Danish bulls back into Danish EBVs.

Table 8. *American PTAs for Danish bulls converted into Danish EBVs*

	Heterosis subtracted			Direct conversion		
	Milk	Fat	Protein	Milk	Fat	Protein
FYN Aalbaek	96	92	103	102	104	108
FYN Haug	104	114	109	110	120	113
FYN Tved	100	111	102	106	115	107
FYN Index	93	103	98	99	108	103
Average	98.3	106.5	103.0	104.3	111.8	107.8

If the assumed positive effect of heterosis is not included in the estimation of the BVs, the genetic merit of bulls from an imported breed will always be overestimated. When a breed is first imported, overestimations will be approx. twice the effect of heterosis. When crossbreeding is carried into subsequent generations, dams will also have genes from the imported breed, and the overestimation will be reduced.

Overestimations of foreign breeds will not be avoided by applying linear models, cf. Table 5. Young bulls, which have genes from the imported breed, will be overestimated on account of heterosis - the effect being proportional to the degree of heterosis expressed in the daug hters. A correct calculation of conversion factors requires the EBVs not to be biased by heterosis.

Import of Genes from New Breeds

The need to consider heterosis is most pronounced when a foreign breed is first imported. At that time it is, however, not possible to partition heterosis from additive heredity. In order to be able to separate the two effects, other crosses in addition to the F_1-crosses are necessary; but at the earliest, they will occur one generation later. Until it becomes possible to calculate reliable heterosis estimates, there are two possible strategies, each with potential advantages and disadvantages:

- Disregard the effect of heterosis
- Fix the effect of heterosis as the average heterosis occuring in crosses with other breeds.

Disregarding heterosis will favour breeds in which the heterosis effect is large in relation to domestic breeds. The extent to which such breeds are favoured will depend on whether heterosis is included for other breeds, or whether heterosis among all breeds is disregarded. If heterosis is included for other breeds, the overestimation of imported bulls will amount to approx. twice the genetic standard deviation. If the heterosis effect is disregarded, the percentage of genes in the bulls from different ancestral sources and the average heterosis effect will be of crucial importance in relation to overestimation. In Table 9 sample calculations for RDM are presented. The breed proportion in the dams was fixed at 75% RDM and 25% ABS. The bulls that make up the base had 75% ABS and 25% RDM. Daughters of average bulls will express a heterosis of 9.6 kg protein, whereas RHF and SRB bulls will express a heterosis 17.6 kg protein and 7.6 kg protein, respectively. It must, however, be assumed that the estimated heterosis effects are true values. Daughters of RHF bulls will express 8 kg more protein due to heterosis than the breed average, while SRB daughters will express 2 kg protein less.

If the heterosis effect is fixed at the average heterosis of crosses with other breeds, the genetic level of the imported breed is likely to be biased. E.g. if the average heterosis effect (RDM x SRB) is approx. 16 kg protein (Table 3), but the true heterosis is 5.6 kg protein, the EBV of SRB bulls will be underestimated by approx. 20 kg protein.

Fixing the heterosis effect on the basis of the relationship among breeds is difficult and unreliable. But breeds of common origin, like e.g. the Jersey breeds in the USA, New Zealand and Denmark or the Holsteins worldwide, show less heterosis when crossed with each other than when crossed with other breeds. The same would be expected with the Angler breed in Schleswig Holstein and RDM.

How to treat newly imported breeds when estimating BVs will also represent a problem in the future when cattle breeding will become still more international. In recent years semen from Montbéliarde bulls has been imported to be used on RDMs, and the heterosis effect between these breeds is unknown.

Table 9. *Average heterosis effect for protein in daughters of bulls of different breeds used for RDM*

Assumptions:

Heterosis: As estimated in table 3
Breed composition in dams: 75% RDM, 25% ABS
Breed composition in average young bulls: 25% RDM, 75% ABS

Heterosis in daughters

Average young bulls:	9.6 kg protein
RHF bulls:	17.6 kg protein
SRB bulls:	7.6 kg protein

Discussion and Conclusion

In this paper it is illustrated that both foreign bulls and progeny tested bulls may be incorrectly ranked if the heterosis effect is disregarded. For RDM, correlations among EBVs with and without correction for heterosis were considerably below 1.00, indicating that breeding decisions based on biased EBVs might lead to a lower genetic progress than expected. The calculation of conversion formulas based on EBVs from a model without heterosis will lead to an overestimation of the imported breed. The need to consider heterosis is most pronounced when the foreign breed is first imported; an estimation of the heterosis effect is, however, not possible at that time. The only possibility seems to be to estimate the effect of heterosis based on the average heterosis estimated in crosses with other breeds.

It is shown that EBVs and DYD-values change over time with changing breed composition in the dams, if they are calculated from a model without heterosis. If heterosis is present, the methods used by "Interbull" to check the data quality, will most likely reject data from a model, that does not take heterosis into consideration, as environmental and genetic trends will be incorrectly separated. It should, however, be further investigated whether the conclusions to be drawn from this analysis, concerning the extent of the over- or underestimation of the genetic and environmental trends, are also correct when heterosis is left out of the model for the estimation of BVs.

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