

Inbreeding Adjustments and Effect on Genetic Trend Estimates

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Introduction

Inbreeding affects both phenotypic means and genetic variances within populations and limits genetic progress even in very large populations (Goddard and Smith, 1990). As average inbreeding increases, routine evaluations may need to model the effects on both the means and the variances. Some national genetic evaluations have included non-additive genetic effects, such as heterosis and recombination between breeds or between North American Holsteins and European Friesians, but few have included inbreeding depression except in research studies (Interbull, 2005).

Changes in genetic variance can be modeled fairly easily once inbreeding coefficients are calculated. Algorithms to construct relationship inverses (\mathbf{A}^{-1}) can either ignore parent inbreeding, resulting in an approximate inverse (\mathbf{A}_0^{-1}), or include parent inbreeding, providing an exact \mathbf{A}^{-1} . Assumed genetic variance and bull rankings were only slightly affected by use of \mathbf{A}_0^{-1} instead of \mathbf{A}^{-1} when inbreeding averaged only 0.01 to 0.04 (Casanova *et al.*, 1992; Wiggans *et al.*, 1995).

Inbreeding depression is a genetic effect that should not simply be removed as if an environmental effect. Instead, predicted transmitting ability (PTA) should include the average expected inbreeding depression and measure the average value of genes when the animal is mated at random to the current population (VanRaden and Smith, 1999). Adjustments to published PTA help to control inbreeding, and additional control is possible by limiting relationships among the specific animals selected (Meuwissen, 1997; Weigel, 2001) and by mating cows non-randomly to less related bulls within herds (Weigel and Lin, 2000).

This study describes adjustments for inbreeding and for differing parity variances

that were introduced in several United States trait evaluations in February 2005. Resulting effects on domestic and foreign genetic trend estimates were quantified and compared with genetic trend tests.

Methods

Selection changes the average relationship of an animal to the population across time, and inbreeding adjustments can account for differences between past inbreeding and expected future inbreeding (EFI). For example, Holstein bull Arlinda Chief (U.S. registration number 1427381, born 1962) had average daughter inbreeding of only 0.3%, but his EFI based on random mating to current 3-year-old cows is 7.4%. In February 2005, his PTA had the largest adjustment for inbreeding, a decrease of 7 pounds for protein.

A regression on inbreeding in the animal model produces PTA adjusted to an inbreeding of 0 (PTA₀). The corresponding daughter yield deviation adjusted to an inbreeding of 0 (DYD₀) is a weighted average of yield deviations adjusted to an inbreeding of 0 (YD₀):

$$YD_0 = y - m - p - c - b(F_{cow})$$

where y = data, m = effect of management group, p = effect of permanent environment, c = herd by sire interaction, b = regression coefficient, and F_{cow} = inbreeding of cow, and

$$DYD_0 = \Sigma w(YD_0 - \text{mate PTA}_0) / \Sigma w$$

where w = a weight. The original weighting factors of VanRaden and Wiggans (1991) ignored parent inbreeding and need to be re-derived.

Adjustments for EFI are included in published PTA (PTA_{EFI}) and in supporting statistics such as parent average (PA_{EFI}). To establish a genetic base of 0, adjustments for

EFI were differences from mean EFI of cows born in 2000 (EFI_{base}). For Holsteins, $EFI_{base} = 4.7\%$.

$$PTA_{EFI} = PTA_0 + b(EFI - EFI_{base}),$$

$$PA_{EFI} = PA_0 + b(EFI - EFI_{base}), \text{ and}$$

$$DYD_{EFI} = DYD_0 + b(EFI - EFI_{base}).$$

The EFI for animals with no descendants in the sample population is the average of parent EFI. Therefore, PA_{EFI} is the average of parent PTA_{EFI} as usual. However, for animals with descendants in the sample, the above formula PA_{EFI} is slightly more precise. If breeding values rather than transmitting abilities are adjusted, the regression must be doubled because EFI measures only half the mean relationship to mates. An alternative, which is used in Canada, is to report the mean relationship.

Inbreeding depression was modeled as a simple linear regression even though effects may differ at higher levels (Thompson *et al.*, 2000). Regression coefficients were from Wiggans *et al.* (1995) for production traits and from an average of literature estimates for other traits. Genetic trends for many U.S. traits were compared and tested by applying trend tests 1, 2, and 3 (Boichard *et al.*, 1995) to evaluations with or without inbreeding adjustments.

An adjustment for differing variance across parities was also introduced in February 2005. Traditionally, multiplicative age adjustment factors were assumed to make genetic variances equal across parities. Now, adjustments for heterogeneous variance are separate by parity. After yield records are age adjusted, deviations in parities 1 through 5 are multiplied by factors of 1.06, 0.99, 0.94, 0.89, and 0.86, respectively. Parity variance adjustments for somatic cell score (SCS) are 0.97, 0.99, 1.01, 1.02, and 1.02; for daughter pregnancy rate, factors are 1.03, 1.00, 0.98, 0.97, and 0.96. Trends and trend tests with or without parity variance adjustments also were compared.

Results

Inbreeding levels now are similar around the world because current Holstein bulls in most countries have common ancestry (Table 1). For example, EFI indicates that U.S. cows are just

Table 1. Inbreeding (F) and pedigree completeness (PEC) statistics by country of origin for Holstein bulls born since 1994.

Country	Bulls (no.)	EFI (%)	Bull F (%)	PEC (%)
United States	8941	5.1	4.7	99.9
Germany	5437	4.7	3.9	96.0
The Netherlands	4324	4.2	4.2	96.8
France	3775	4.8	4.5	98.0
Canada	2132	4.9	5.5	99.2
Denmark	2083	4.7	4.0	85.4
Italy	2056	4.9	4.3	96.2
New Zealand	1514	3.5	3.5	82.5
Poland	1473	3.5	2.7	79.5
Australia	1397	4.6	4.1	83.2
United Kingdom	756	4.8	4.6	98.3
Sweden	474	4.6	3.7	88.1
Switzerland	436	3.2	3.1	78.6
Japan	375	5.0	4.6	96.8
Spain	353	5.1	5.0	98.6

as related to Spanish bulls as to U.S. bulls. Among the 15 countries with the most Holsteins, only bulls from New Zealand, Poland, and Switzerland had many different or missing ancestors.

Pedigree completeness (PEC) is the proportion of known ancestors back to 1970, and Table 1 shows that the USDA pedigree file is fairly complete for bulls from most countries. Earlier studies (MacCluer *et al.*, 1983; Sigurdsson and Jonmundsson, 1994; Cassell *et al.*, 2002) defined pedigree completeness as ability of the pedigree to measure the animal's own inbreeding coefficient, whereas the current target is to measure progeny inbreeding. Thus, a pedigree in which the dam is unknown and the sire ancestry is completely known is currently defined to be 50% complete but was defined in the earlier studies to be 0% complete.

Adjustments for inbreeding decreased genetic trend estimates noticeably but had much smaller effects on trend tests. For Holsteins, trend was reduced by 6% for yield traits and 25% for productive life and became 14% more negative for daughter pregnancy rate. Trend for SCS changed little because the regression on inbreeding is small for that trait. For Jerseys, trend was reduced by 9% for yield traits and 32% for productive life and became nearly twice as negative for cow fertility. In Table 2, differences in genetic trend were computed using transmitting ability trends per year divided by genetic standard deviations to allow

Table 2. Changes in genetic trends and trend tests (in genetic standard deviations per year) from inbreeding adjustment for Jerseys.

Trait	Trend change	Trend test differences		
		Test 1	Test 2	Test 3
Protein	-.018	-.005	.000	.001
Fat	-.015	-.001	.000	.000
SCS	.002	.000	.000	.000
Longevity	-.024000	-.005
Fertility	-.009	.001	.001	.001

comparison with trend tests that are required by Interbull to be no larger than 0.01.

Changes in genetic trend were generally larger than the Interbull limit and much larger than any changes in trend test values. None of the three tests identified the large biases from disregarding inbreeding. Test-2 values differed greatly from 0 if PTA_{EFI} was used to predict DYDs that were not adjusted for inbreeding, but test 2 did not detect any change in trend when PTA and DYD from the former model were replaced by PTA_{EFI} and DYD_{EFI} from the new model.

Parity variance adjustments caused small decreases in genetic trend but larger changes in some trend tests (Table 3). If those adjustments had not been applied, U.S. Jersey data for yield and SCS would have been discarded because of Interbull rules. For example, test 1 for protein decreased by .006 from a value of .014 before to .008 after adjustment. Rejection of data is an extremely severe penalty for minor model differences that do not affect national or international rankings.

Correlations between evaluations for recent bulls were above 0.9996 when parity variance adjustments were applied and above 0.997 when inbreeding adjustments were applied,

Table 3. Changes in genetic trends and trend tests (in genetic standard deviations per year) from parity variance adjustment for Jerseys.

Trait	Trend change	Trend test differences		
		Test 1	Test 2	Test 3
Protein	-.004	-.006	-.001	-.002
Fat	-.002	-.003	-.001	.000
SCS	-.002	.000	.000	.000
Fertility	.000	-.001	-.002	-.002

indicating small differences from the adjustments. With both adjustments included in the September 2004 Interbull test evaluation, the average number of United States bulls in the top 100 for protein yield on each country scale increased slightly from 24.5 to 25.3 for Holsteins and from 53.8 to 56.3 for Jerseys, which is surprising because estimated genetic trend in the United States decreased by 6% for Holsteins and 9% for Jerseys.

Genetic trend estimates on other scales also decreased when U.S. evaluations were adjusted for inbreeding and parity variance. Table 4 compares August 2004 with September 2004 test evaluation trends on several scales. Bulls were considered to be from the United States if that was the country with the largest number of daughters and to be from outside the United States (non-United States) otherwise. Genetic trends on U.S. and Canadian scales were slightly higher than on other scales, possibly because those data files include more of the daughters upon which early selection was based. Trend ratios of non-United States to United States bulls changed little on all scales when reduced trends were introduced in U.S. evaluations (September 2004 test evaluations). Multi-trait across-country evaluation (MACE) appears to be robust to trend biases when countries are well connected.

Table 4. Estimated trends (genetic standard deviations per year) for United States and non-United States Holstein bulls on various scales before (August 2004) and after (September 2004) U.S. model changes for inbreeding and parity variance adjustments.

Scale	August 2004 trend			September 2004 trend		
	United States	Non-United States	Ratio ¹	United States	Non-United States	Ratio ¹
Canada	.215	.243	1.13	.209	.234	1.12
France	.189	.221	1.17	.184	.218	1.18
Germany	.178	.214	1.20	.173	.211	1.22
The Netherlands	.182	.219	1.20	.177	.214	1.21
United States	.231	.239	1.03	.222	.226	1.02

¹Trend for non-United States bulls divided by trend for United States bulls.

Conclusions

Inbreeding adjustment had large effects on genetic trends but only small effects on trend tests. Parity variance adjustments had small effects on genetic trends but larger effects on method-1 trend tests. For both adjustments, trend tests were not good indicators of trend problems. The U.S. genetic trend for longevity is higher than in most other countries, but the trend tests did not allow the USDA to adjust productive life for inbreeding, which would reduce U.S. productive life trend by 25% and provide more accurate evaluations.

Boichard *et al.* (1995) stated that biased genetic trend “strongly disturbs international germplasm exchanges based on conversion formulas...” However, biases within country cause fewer problems with MACE than with the old conversion formulas because MACE allows re-ranking across country scales. When the PTA of a bull such as Blackstar (U.S. registration number 1929410) is adjusted downward on the U.S. scale because he has the highest EFI (7.9%), MACE also reduces the PTAs of Blackstar sons proven in other countries when converting their evaluations from the foreign to U.S. scale and increases the evaluations of U.S.-proven Blackstar sons when converting those to other country scales.

Similarly, MACE partially adjusts for differences in genetic trend. Researchers may want to test genetic trends, but national data files should not be rejected based on those tests. A more inclusive and friendly approach is needed. Adjustments for inbreeding, differing parity variance, etc., may be helpful but should not be required.

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