

HETEROGENEITY AMONG FAMILIES OF HOLSTEIN CATTLE IN INBREEDING DEPRESSION FOR PRODUCTION TRAITS

Filippo Miglior, E. B. Burnside, and W. D. Hohenboken¹

Centre for Genetic Improvement of Livestock, Dept. of Animal and Poultry Science,
University of Guelph, Guelph, Ontario, N1G 2W1, Canada

¹ Dept. of Animal and Poultry Science, Virginia Polytechnic Institute and State University
Blacksburg, Virginia, 24061, USA

SUMMARY

First lactation records from 58,433 Holstein cows were analyzed to investigate the presence of variability of inbreeding depression for production traits among families tracing to different common ancestors. A total of 48 common ancestor families were identified. An animal model that included an interaction between family and inbreeding depression of the descendants was fitted for milk, fat and protein yield, and fat and protein percent. The interaction was significant for milk, fat and protein yield. Thus, heterogeneity of inbreeding depression was evident for the three yield traits, suggesting that the founders did differ substantially in response of their descendants to inbreeding. The average values of the slopes of inbreeding depression of the 48 families were very similar to the common slope and were within literature estimates for all traits. Variability in inbreeding depression may arise if founders of a family vary in number of deleterious recessive genes. When a common slope is fitted in the model to take account of effects of inbreeding, genetic evaluations will yield erroneous estimates, if variability of inbreeding depression among families is present.

INTRODUCTION

Several studies have reported effects of inbreeding on quantitative traits and have been summarized by Pirchner (1985). Linear regression of performance on inbreeding is the most commonly used method to measure inbreeding depression. Usually, a common slope is fitted to account for decreased performance due to the level of inbreeding. However, inbreeding is a sampling process, and founders of a family may differ in the number and effect of deleterious recessive genes, thus affecting the magnitude of inbreeding depression in the descendants. Few studies have looked for evidence of variability of inbreeding depression among sub-lines. Mi et al. (1965) studied effects of inbreeding on dairy production traits in six sire lines. They concluded that heterogeneity of inbreeding depression was present among the Holstein sire-lines, with ranges in estimates from -1 to -88 kg for mature equivalent milk yield and from 0 to -2.64 kg for mature equivalent fat yield for each 1% increase in inbreeding. Beckett et al. (1979) looked at different traits in six sire lines in dairy cattle, and found significant variability of effects of inbreeding among sire lines only for reproductive traits. Hohenboken et al. (1991) examined variability among families of *Tribolium castaneum* in inbreeding depression for fitness traits. The experiment provided evidence that, for certain fitness traits (e.g. larval weight), males differed in the response of their progeny to inbreeding. It was concluded that these males differed in the number and effects of recessive genes affecting these traits.

The objective of this study was to investigate in a dairy cattle population the presence among founders of heterogeneity of inbreeding depression for production traits.

MATERIALS AND METHODS

First lactation records (92,838 cows) analyzed in Miglior et al. (1994) were edited to create a data subset to investigate heterogeneity among individuals in inbreeding depression of their descendants. Individual inbreeding coefficients of all cows were computed previously (Miglior and Burnside, 1994). The algorithm to compute inbreeding coefficients by Miglior et al. (1992) was modified to identify all common ancestors for each animal. The common ancestor bull with the highest additive genetic relationship to

each inbred cow was then determined. Records were eliminated when there were fewer than 100 inbred descendants of such common ancestors. After this editing, 48 bulls with 58,433 first lactation descendant records remained.

Descriptive statistics for milk, fat and protein yield, fat and protein test and inbreeding coefficients are shown in Table 1. Distribution of cows by level of inbreeding coefficient is shown in Table 2.

Table 1. Descriptive statistics for the production traits and inbreeding coefficient.

Variable	Average	SD [‡]	Minimum	Maximum
305-d Milk (kg)	6793	1221	1238	13666
305-d Fat (kg)	257	48	46	575
305-d Fat test (%)	3.78	.43	1.61	6.40
305-d Protein (kg)	219	39	40	418
305-d Protein test (%)	3.22	.22	1.15	5.28
Inbreeding (%)	3.40	2.71	.03	26.23

n = 58433

[‡]Standard Deviations

Table 2. Distribution of cows by level of inbreeding coefficient (F).

Class of Inbreeding (%)	% of Cows
0 < F < 6.25%	77.00
6.25% ≤ F < 12.5%	21.76
12.5% ≤ F < 18.75%	1.21
18.75% ≤ F < 25%	.02
F ≥ 25%	.01

A pedigree file of 195,440 animals was used in the analysis. The additive animal model used in the analysis was:

$$y_{ijkm} = h_i + bF_j \times c_k + a_j + e_{ijkm}$$

where:

y_{ijkm} : first lactation 305-d, 2x milked, records for milk, fat and protein yield, and fat and protein percent from 58,433 cows born between 1982 and 1991 (records were preadjusted for age and month of calving),

h_i : fixed effect of i_{th} herd-year-season of calving,

bF_j : linear regression of the trait on inbreeding coefficient of j_{th} animal,

c_k : fixed effect of the k_{th} common ancestor,

a_j : random effect of animal $j \sim (0, A^{-1} \sigma_a^2)$ where A is the numerator relationship matrix (including inbreeding) among animals and

e_{ijkm} : residual variance associated with the record $m \sim (0, I \sigma_e^2)$.

A second model, in which $bF_j \times c_k$ was replaced by bF_j , was fitted to test significance of the interaction. The computing strategy of Schaeffer and Kennedy (1986) was used to fit the models. The solutions were found by Gauss-Seidel iteration with a relaxation factor on the animal solution. Heritabilities used in the mixed model equations were .29, .29, .24, .55 and .68 for milk, fat and protein yield, and fat and protein percent, respectively (Miglior et al., 1994).

RESULTS AND DISCUSSION

Reduction in sums of squares due to the interaction of common ancestor with inbreeding coefficient was tested for significance with an F-test. The interaction was significant for milk, fat and protein yield ($p < .0001$), indicating that common ancestors did differ substantially in response of their descendants to inbreeding. Averages, standard deviations and ranges for inbreeding depression within descendants of the 48 common ancestors are reported in Table 3. Average values of inbreeding depression of the common ancestors (model 1) were very similar to the common slope (model 2) and were within range of literature estimates for all traits. Coefficients of variation were about 60% for the yield traits. Similar values, in terms of size of coefficients of variation, were found by Hohenboken et al. (1991). Mi et al. (1965) suggested that variability of inbreeding depression among sire-lines, could be due to differences in average inbreeding levels among lines. However, their experimental lines, which had approximately the same degree of inbreeding, also showed differences in magnitude and direction of effects of inbreeding on various traits. In this study, average inbreeding levels varied among common ancestor lines (from 1 to 9%). However, samples were large for each family and regressions were independent from the average inbreeding levels within family. Brewer et al. (1990) conducted an experiment on variability of inbreeding depression on fitness in laboratory stocks of mice. Responses to inbreeding were highly different: some populations had smaller litters, others experienced higher mortality, some showed slower growth rates, and one displayed no significant effects, when inbred. They concluded that inbreeding depression may be controlled by a small number of genes and that the genetic load depends on which alleles are present in the founders of a population.

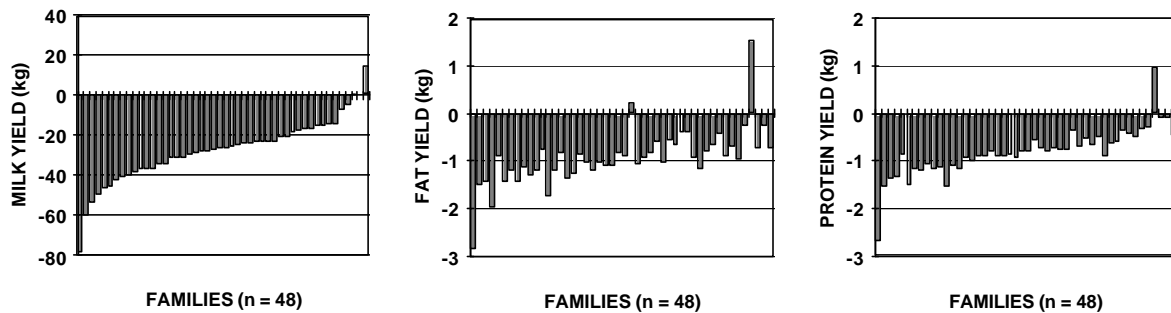
Variability of inbreeding depression will influence genetic evaluations. It has been proposed (Kennedy and Sorensen, 1988; VanRaden, 1990) to include the inbreeding coefficient of the animal as a covariate in genetic evaluation models, to take account of inbreeding depression. However, when variability of inbreeding depression is present a common slope would penalize those families that had more inbreeding depression than average, and benefit those that had less inbreeding depression.

Table 3. Averages, standard deviations, and ranges for inbreeding depression in 48 families for milk, fat and protein yield (reduction per 1% increase in inbreeding coefficient).

	Milk (kg)	Fat (kg)	Protein (kg)
Model 2 - common slope	-27.7	-0.99	-0.87
Model 1 - 48 slopes			
Average	-27.9	-0.96	-0.84
Std. Deviation	16.1	0.61	0.52
Std. Error	2.3	0.09	0.08
Coeff. of Variation (%)	57.5	63.60	61.41
Minimum	-79.0	-2.88	-2.71
Maximum	14.6	1.55	0.98

Figure 1 shows the effects of inbreeding on milk, fat and protein yield for the 48 families, per 1% increase in inbreeding coefficient. Values are sorted by regression of milk yield on inbreeding coefficient. Some changes in the rank of the ancestors are visible for inbreeding depression of milk, fat and protein yield. Inbreeding depressions for protein yield are highly correlated with fat (.87) and milk (.86) yield. However, milk and fat yield inbreeding depressions are less correlated at .70. Overall, families that had greater inbreeding depression for milk yield also had greater depression for fat and protein yield.

Figure 1. Effect of inbreeding on milk, fat and protein yield among families (reduction per 1% increase in inbreeding coefficient). Values are ranked by regression of milk yield on inbreeding.



CONCLUSIONS

The interaction of common ancestor by inbreeding coefficient was significant for milk, fat and protein yield. Average values of inbreeding depression were very similar to the common slope and were within literature estimates for all traits. Responses to inbreeding were highly variable, thus suggesting that common ancestors did differ substantially in response of their descendants to inbreeding. Overall, magnitudes and directions of inbreeding depression among the common ancestors were consistent across the yield traits. Variability of inbreeding depression among common ancestors may be due to differences in initial proportion of heterozygous loci. Thus, inbreeding depression may be determined by relatively few recessive genes, and the inbreeding depression in the descendants may depend on which alleles are present in the founders of a population. Fitting a common slope to take account for inbreeding depression in genetic evaluations may not be adequate, in presence of heterogeneity of inbreeding depression.

ACKNOWLEDGMENTS

This research has been supported by the Ontario Ministry of Agriculture and Food, Agriculture Canada through a research contract, and the Natural Sciences and Engineering Research Council of Canada. The authors acknowledge the very important technical support by Dr. Gerald Jansen, who modified the algorithm to allow the identification of common ancestors. The authors acknowledge also the helpful comments in reviewing this paper by the other members of the Ph.D. committee: Dr. J. C. M. Dekkers, Dr. B. W. Kennedy, Dr. W. S. Martin, and Dr. C. Smith.

REFERENCES

- BECKETT, R. C., LUDWICK, T. M., RADER, E. R., HINES, H. C., and PEARSON, R. (1979). *J. Dairy Sci.* 62:613-620.
- BREWER, B. A., LACY, R. C., FOSTER, M. L., and ALAKS, G. (1990) *J. Heredity* 81:257-266.
- HOHENBOKEN, W. D., KOCHERA, Y., and DAWSON, P. S. (1991) *J. Anim. Breed. Genet.* 108:446-454.
- KENNEDY, B. W., and SORENSEN, D. A. (1988) *Proc. 2nd Int. Conf. Quant. Genet.* p.91.
- MI, M. P., CHAPMAN, A. B., and TYLER, W. J. (1985) *J. Dairy Sci.* 48:77-84.
- MIGLIOR, F., SZKOTNICKI, B., and BURNSIDE, E. B. (1992) *J. Dairy Sci.* 75:1112-1118.
- MIGLIOR, F., and BURNSIDE, E. B. (1994) *J. Dairy Sci.* submitted.
- MIGLIOR, F., BURNSIDE, E. B., and KENNEDY, B. W. (1994) *J. Dairy Sci.* submitted.
- PIRCHNER, F. (1985) In: A. B. Chapman (ed.) *General and Quantitative Genetics.* World Animal Science A4, Elsevier, Amsterdam, pp. 227-250.
- SCHAEFFER, L. R., and KENNEDY, B. W. (1986) *J. Dairy Sci.* 69:575.
- VanRADEN, P.M. (1990) *Proc. 4th World Congr. Genet. Appl. Livest. Prod.*, Edinburgh, UK, XIII:357