ANALYSIS OF GAMETIC IMPRINTING EFFECTS FOR TEST DAY MILK YIELD IN AUSTRALIAN HOLSTEIN CATTLE

C. J. Kaiser, M. E. Goddard, and A. Reverter

Animal Genetics and Breeding Unit, University of New England, Armidale NSW 2351
AGBU is a joint initiative of UNE and NSW Department of Agriculture

SUMMARY
Adjusted test day milk yields from 19,688 first parity, Friesian heifers were analyzed to determine if either paternal and maternal gametic imprinting were important sources of variation in Australian dairy cattle. Paternal imprinting accounted for 1% of the variance in adjusted milk yield, while maternal imprinting accounted for .5%. Neither additive nor residual variances were greatly affected by including gametic imprinting in the model. Heritability estimates from analyses without gametic imprinting and with sire or maternal imprinting were .283, .262, and .276, respectively. These results suggest gametic imprinting does not cause variation in milk yield in Australia.
Keywords: Gametic imprinting, variance components, Method R, dairy.

INTRODUCTION
In dairy cattle, estimates of genetic parameters and predictions of breeding value are usually based on an additive genetic model. However, Visscher and Thompson (1990) found results inconsistent with this model in that the "female" heritability (h^2) was .477, while the "male" h^2 was .280. These results could be due to modes of inheritance other than additive Mendelian inheritance influencing milk yield. One possibility is gametic imprinting, in which only the allele inherited from one parent is expressed. Significant paternal imprinting effects for backfat thickness and growth rate in pigs have been reported (de Vries *et al.*, 1994). Accounting for these effects should not only improve breeding value estimation, but could also result in additional performance from selecting parents based upon maternal or paternal gametic imprinting values.

The objective of this study was to determine if gametic imprinting affected test day milk yield in the Australian Friesian dairy herd.

MATERIALS AND METHODS
Data selection. The Australian Dairy Herd Improvement Scheme provided test day and pedigree data for this analysis. Selected records consisted of second quarter, first lactation milk yields for Friesian cows recorded from 1980 to 1996, plus all available pedigree information. The full data set was edited to ensure accuracy and to select herds with complete pedigree and test day information. Milk yields were then adjusted for the affects of age at calving, days in milk, and days bred, using previously calculated additive adjustment factors (unpublished data).

To simplify the analysis, a single record was chosen from each animal as follows. All of the records in the largest herd test day (HTD) contemporary group were selected. All other records from the cows in that group were eliminated from the full data set and then the records from the largest remaining HTD were selected. The process was repeated until all remaining HTD had fewer than ten records, at which point the remaining records were discarded. The selected data set consisted of 193,809 milk yields, recorded on 10,715 HTD from 1,495 herds. From this data set, we took a random subsample, consisting of 152 herds, with 1,043 HTD, and 19,688 records. We then added all recorded ancestors of these animals to give a pedigree of 37,964 animals.

Analysis. Variance components were estimated under three scenarios for the analytical model
$$y = X \beta + Z_u u + Z_g g + e$$
where y is the vector of adjusted test day milk yields, β is a vector of fixed HTD effects, u, g, and e are random vectors of additive genetic effects due to the animal, imprinting effects due to the parental gametes, and errors, respectively, and X, Z_u, and Z_g are incidence matrices relating corresponding effects to records. Random components were distributed

$$\begin{bmatrix} u \\ g \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & G\sigma_g^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where A is Wright's numerator relationship matrix, G is the relationship matrix for all animals in A augmented with either the paternal or maternal gamete of animals with records (Schaeffer *et al.*, 1989; Tier and Sölkner, 1993), I is the identity matrix, and σ_a^2, σ_g^2, σ_e^2 are additive, gametic, and error variances, respectively. The first and second analyses estimated variance due to paternal and maternal gametic imprinting effects, respectively, while the third analysis eliminated gametic imprinting effects to gauge their effect on additive variance estimates.

We used Method R procedures with multiplicative adjustments to estimate variance components (Reverter *et al.*, 1994). Twenty 50% samples were evaluated for each model, with solutions considered converged when the relative change in each variance component was less than 10^{-4}.

For the two gametic imprinting models, heritability (h^2), and the proportion of variance due to gametic imprinting (g^2) were calculated for each set of estimates. These pairs of ratios were sampled with replacement to obtain a bootstrap data set of N = 1000 pairs (Efron and Tibshirani, 1993). We transformed this data set to an approximately normal scale by choosing the power transformations which maximized the probability the transformed variables belonged to a joint normal distribution (Box and Cox, 1964). The means and estimation error covariance matrix were then computed from the transformed variables. Contour lines for 25, 50, 75, 90, and 95% of the joint density were calculated and then back-transformed to the original scale.

RESULTS AND DISCUSSION

Table 1 contains the mean estimates of the variance components and ratios for each model. Gametic imprinting accounted for less than one percent of the total variance in both the sire and dam models, while heritabilities were similar under all three models. The decrease in σ_a^2 associated with fitting gametic imprinting was about the same as σ_g^2 for the maternal imprinting analysis, but just over 2.5 times σ_g^2 for the paternal imprinting analysis. In the absence of gametic imprinting, if one were to fit gametic effects instead of additive genetic effects, the expectation of σ_g^2 would be twice σ_a^2 (Tier, personal communication). Thus, the gametic effects may have accounted for some increased covariance between half-sibs which had previously gone to additive variance. The very low magnitude of σ_g^2 in both models suggests that this increased covariance was either very small, or was of a different structure, such as an interaction between sires and contemporary groups.

Table 1. Variance components and proportion of phenotypic variance due to additive genetic effects (h^2) and gametic imprinting effects (g^2)

Model	σ_p^2 (liters^2)	h^2	g^2
Animal[a]	8.027 ± .431	.283 ± .022	--
Sire[b]	7.920 ± .392	.262 ± .030	.010 ± .007
Dam[c]	8.105 ± .362	.276 ± .029	.005 ± .007

[a]Analysis of only additive genetic effects due to the animal.
[b]Analysis of additive genetic effects due to the animal plus paternal gametic imprinting effects.
[c]Analysis of additive genetic effects due to the animal plus maternal gametic imprinting effects.

The joint distribution of h^2 and g^2 for the sire gametic model is illustrated in Figure 1. The distribution is positively skewed and g^2 is near zero for much of the range of h^2. The joint distribution for the maternal gametic imprinting model could not be drawn because the estimate for g^2 was so strongly skewed towards zero. Seven of the twenty g^2 estimates were less than .001 and only five were greater than .01. Because of this the power transformation needed to maximize normality was less than -35. Approximating the joint distribution with these transformed variables resulted in much of it lying outside of the parameter space.

This research sought to identify whether gametic imprinting increased the covariance between records of certain classes of relatives beyond what is predicted from a purely additive model. This is of special concern in dairy evaluations where most of the information on young sires comes from only paternal half-sibs. If daughters of certain bulls were selected as replacement dams, based on paternal imprinting effects, the next generation would not perform as well, thus slowing genetic progress. However, the small magnitude of gametic imprinting variances observed in this data set indicates excluding imprinting from the analysis would not create important levels of bias.
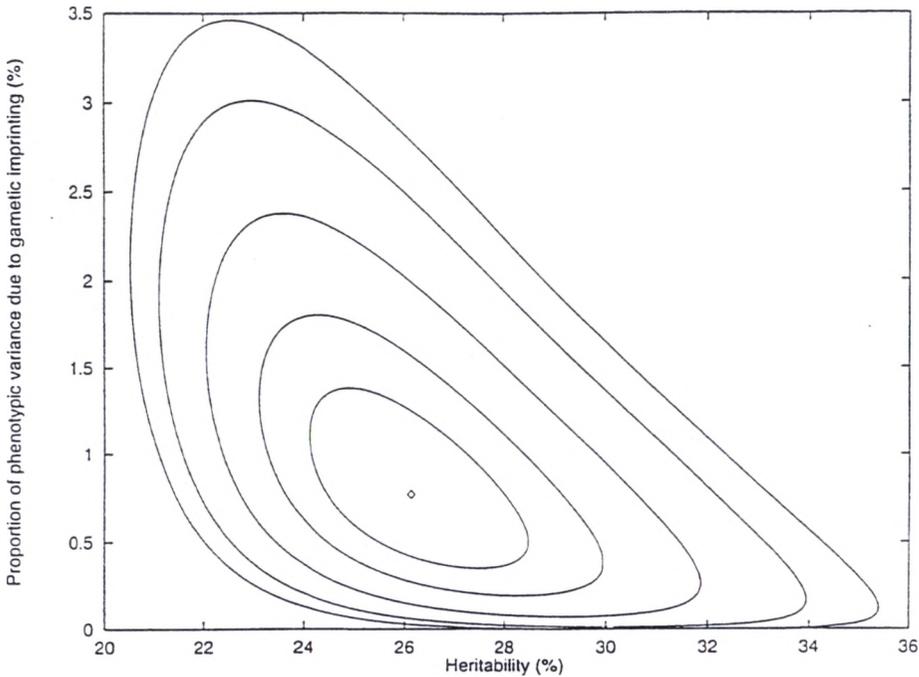
Figure 1. Approximate joint probability density function (pdf) for proportion of phenotypic variance accounted for by paternal gametic imprinting and additive genetic variance (heritability). Contour lines represent 25, 50, 75, 90, and 95 % of pdf.

REFERENCES
Box, G. E. P., and D. R. Cox. (1964) J Royal Stat. Soc. (B) **26(2)**:211-252.
de Vries, A. G., Kerr, R., Tier, B., Long, T., and Meuwissen, T. H. E. (1994) *Theor. Appl. Genet.* **88**:1037-1042.
Efron, B. and Tibshirani, R. J. (1993) "An Introduction to the Bootstrap" Chapman & Hall, New York.
Reverter, A., Golden, B. L., Bourdon, R. M., and Brinks, J. S. (1994) *Proc. 5th World Cong. Gen. Appl Livest. Prod.* **18**:406-409.
Schaeffer, L. R., Kennedy, B. W., and Gibson, J. P. (1989) *J. Dairy Sci.* **72**:1266-1272.
Tier, B., and Sölkner, J. (1993) *Theor. Appl. Genet.* **85**:868-872.
Visscher, P. M. and Thompson, R. (1990) *Proc. 4th World Cong. Gen. Appl Livest. Prod.* **14**:233-236.