Systematic Error in Genetic Evaluation of Miles City Line 1 Hereford Cattle Resulting from Preadjustment for Age of Dam[1]

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ABSTRACT: Differences in preweaning growth of calves nursing 2- and 3-yr-old dams compared with contemporaries nursing older dams are accentuated in the Miles City Line 1 Hereford herd relative to age-of-dam (AOD) effects implied by preadjustment of 205-d weight in national cattle evaluation. Mixed-model analyses of 205-d weight that fit random individual direct effects and maternal genetic and permanent environmental effects on 4,998 calves were conducted to 1) determine the magnitude of residual AOD effects after preadjustment (PA) using industry-standard procedures and 2) compare changes in genetic predictions resulting from either PA or simultaneous adjustment (SA) for AOD. Expressed as differences from the 5- to 10-yr-old age effect, simultaneously estimated AOD effects were 45 ± 1, 19 ± 1, 6 ± 1, and 19 ± 3 kg for 2, 3, 4, and 11+ AOD classes, respectively. Comparable estimates of residual AOD effects after PA were 20 ± 1, 6 ± 1, 1 ± 1, and 14 ± 3 kg. Rank correlations of direct (BV_d) and maternal (BV_m) breeding values (BV) for 205-d weight from the analysis using PA with BV predicted using SA for AOD were .98 and .77, respectively. Estimated genetic trends were also affected by the method of accounting for AOD effects. One hundred fifty replicate simulations of 205-d weights with pedigree, fixed effect, and variance-covariance structures corresponding to the experimental population were used to establish correlations (r) of predicted BV with underlying true values. The r of predicted BV_d with true values were reduced less than .02 by PA compared to SA in accounting for AOD. However, r of predicted BV_m with true values were reduced more than .13 by PA compared to SA in accounting for AOD. These data indicate potential for systematic error in genetic evaluations that apply standard adjustments for AOD to 205-d weight.

Key Words: Genetic Improvement, Beef Cattle, Maternal Effects, Best Linear Unbiased Estimation, Errors

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Introduction

Breed-wide genetic evaluation of Hereford cattle (BIF, 1990) results in BLUP of direct (**BV_d**) and maternal (**BV_m**) breeding values for 205-d weight preadjusted for age-of-dam (**AOD**) effects. However, inaccurate preadjustment and subsequent omission of AOD effects from statistical models used in genetic evaluation may introduce systematic error in selection of breeding stock (Nelsen and Kress, 1981). MacNeil et al. (1992) observed AOD adjustment factors necessary to correct calf weaning weight records from 2- and 3-yr-old Line 1 Hereford dams to a mature equivalent basis exceeded those routinely employed in evaluating Hereford cattle (American Hereford Association, 1992). The Miles City Line 1 population has been an important contributor to the Hereford breed (Dickenson, 1984), and thus its genetic evaluation free from systematic error is particularly important.

This research was conducted to determine effects on BV_d and BV_m of preadjustment (**PA**) of 205-d weight for AOD relative to simultaneous adjustment (**SA**). Similarity of genetic predictions using PA and SA were tested with performance records from the Miles City Line 1 Hereford herd. Relationships between true and predicted BV using PA and SA for AOD effects were compared in simulated data.

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Materials and Methods

Management of Livestock. The Miles City Line 1 Hereford population was founded primarily on two paternal half-sib sires, Advance Domino 20th and Advance Domino 54th, that first produced progeny in 1935. The herd was closed at that time. Resulting daughters of each sire were mated to the other half-sib sire. Subsequent sire selection has emphasized post-weaning growth.

Data used in this research were collected from 1935 to 1989. Most management practices have remained reasonably constant throughout the period. Throughout the year, cows grazed native ranges composed of predominantly western wheatgrass, Sandberg bluegrass, blue gramma grass, buffalo grass, needle-and-thread, green needle grass, annual brome grasses, thread leaf sedge, greasewood, and silver and big sagebrush. Annual precipitation averages 34 cm, with 21 cm occurring from March to July. Each year the cows were moved to winter pasture approximately January 1 and provided with varying amounts of protein and energy supplements, and hay was fed if snow cover prevented normal winter grazing. Calving began in mid- to late March. Calving of 2-yr-old heifers was initiated in 1972. Before 1972 the initial calving was at 3 yr of age. Calves were routinely weighed within 24 h of birth. A few days after birth cow-calf pairs were moved to native range, then divided into single-sire breeding herds in early June. Heifers were exposed to the same bulls at the same time as the older cows each year. After the breeding season ended in early August, cows and calves moved to summer range. Calves were not creep fed. Weaning occurred in mid-October when all calves were weighed at an approximate average age of 180 d. More details pertaining to management of the cattle, the environment in which they have been raised, and the Line 1 Hereford population are in MacNeil et al. (1992).

Statistical Analyses of Data. The data used for this study were performance records from 4,998 calves that were progeny of 195 sires and 1,493 dams. The dams were themselves progeny of 175 sires. For each calf, a 205-d weight was computed from its birth weight and average daily gain from birth to weaning. American Hereford Association (1992) Total Performance Records (**TPR**) adjustments for AOD were computed for the record of each calf using the series of quadratic regressions on days of age of each dam for bull and heifer calves that had not been fed creep. The interaction of sex with AOD was included in TPR procedures.

Individual-animal, mixed-model analyses were conducted using the following linear model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_{d}\mathbf{u}_{d} + \mathbf{Z}_{m}\mathbf{u}_{m} + \mathbf{Z}_{pe}\mathbf{u}_{pe} + \mathbf{e}.$$

In this general model, $\mathbf{X}$ is a matrix relating a vector of fixed effects ($\boldsymbol{\beta}$) to the dependent variable ($\mathbf{y}$). Fixed effects in analysis 1 were contemporary groups defined as year by sex of calf subclasses, a separate discrete classification for age of dam (2, 3, 4, 5 to 10, and 11+ yr of age), and linear regressions on inbreeding of calf and dam. The dependent variable in analysis 1 was 205-d weight without preadjustment for age of dam. Analysis 2 was similar to analysis 1, except that the dependent variable was 205-d weight preadjusted for AOD effects. The data and linear model used in analysis 3 were similar to analysis 2, except that AOD was omitted from the model. The interaction of sex by AOD has been consistently small and not important in this and other analyses of data from the Miles City Line 1 Hereford population (MacNeil et al., 1992; Snelling et al., 1996). It has not been included in any of the statistical analyses reported here.

Also in the above model, $\mathbf{Z}_d$ is an incidence matrix relating random BV_d ($\mathbf{u}_d$) to $\mathbf{y}$; $\mathbf{Z}_m$ is an incidence matrix relating random BV_m ($\mathbf{u}_m$) to $\mathbf{y}$; $\mathbf{Z}_{pe}$ is an incidence matrix relating random permanent environmental effects due to dams ($\mathbf{u}_{pe}$) to $\mathbf{y}$; and $\mathbf{e}$ is a vector of random residual effects. Except for the covariates, all elements of the $\mathbf{X}$ and $\mathbf{Z}$ matrices were either 0 or 1. The assumed variance-covariance structure was as follows:

$$\mathrm{Var}\begin{bmatrix}\mathbf{u}_d\\ \mathbf{u}_m\\ \mathbf{u}_{pe}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{dm} & 0 & 0\\ \mathbf{A}\sigma_{dm} & \mathbf{A}\sigma_m^2 & 0 & 0\\ 0 & 0 & \mathbf{I}_{pe}\sigma_{pe}^2 & 0\\ 0 & 0 & 0 & \mathbf{I}_e\sigma_e^2\end{bmatrix}$$

where $\mathbf{A}$ is the numerator relationship matrix accounting for all known pedigree ties among individuals and including inbreeding effects and $\mathbf{I}_{pe}$ and $\mathbf{I}_e$ are identity matrices of ranks equal to the number of dams (n = 1,493) and observations (n = 4,998), respectively. Thus, there are some procedural differences between the TPR genetic evaluation and this study. In the TPR genetic evaluation, inbreeding effects on level of performance are not presently accounted for, nor are inbreeding effects on relationships among animals considered in computing A inverse. However, in this study differences between analyses were confined to differences in methods of accounting for AOD effects. The effects of inbreeding on level of performance and on relationships among animals were included in all analyses. Estimates of the population parameters (σ_d^2 = 85.5, σ_m^2 = 113.3, σ_{dm} = −7.8, σ_{pe}^2 = 68.5, and σ_e^2 = 231.3) were derived from the data and model of analysis 1 using the implementation of derivative-free restricted maximum likelihood described by Boldman et al. (1993). These estimates were used throughout this study to avoid confounding changes in genetic evaluations associated with alternative methods of accounting for AOD with changes in the population parameters.

Accuracies of predicted BV were calculated as one minus the ratio of prediction error variance to genetic variance (BIF, 1990). Prediction error variance was obtained from diagonal elements of the inverse of the coefficient matrix (Henderson, 1984).

Breeding values from analysis 1 were compared to their counterparts from analysis 3 to determine effects associated with the alternative methods used for AOD adjustment. Product-moment and rank correlations of paired BV_d and of paired BV_m and changes in rank of predicted BV_d and BV_m between analyses 1 and 3 were calculated. Further, it was expected that if the genetic evaluations of analyses 1 and 3 were similar, then individual animals would be ranked in the same decile by both analyses. Thus, sets containing 10% of the individuals with records were formed based on results from both analysis 1 and analysis 3. Membership in the intersection of these sets was used to quantify important changes in rank without resorting to case studies of individual animals. Similar evaluations were made using both predicted BV of all animals and of the subset of 207 sires and maternal grandsires present in the data. Birth-year mean BV were plotted to illustrate differences between analyses in genetic trends for direct and maternal genetic effects.

Simulation. The methodology of Van Vleck and Gregory (1992) as detailed by Mallinckrodt (1993) was used to simulate 205-d weights with pedigree and fixed effect structures corresponding to the experimental population. Fixed effects were generated from an analysis of the data similar to analysis 1, but incorporating AOD effects into the contemporary group specification. Thus, in the simulations any interactions of year, sex, and AOD present in the experimental population were also included in the simulated data. Random effects were drawn from normal distributions with means of zero and variance-covariance structure as specified previously. Fixed effect constants and simulated random effects replaced the parameters to be estimated in the general model previously described and phenotypes were computed. The simulated data were analyzed using models and procedures previously described for analyses 1 and 3. Upon completion of these analyses, correlations of the resultant predicted BV_d and BV_m with their respective simulated true values were calculated. The simulation procedure was replicated 150 times. Means and standard errors of the correlations between simulated and predicted BV were calculated both for the 4,998 animals with records and for the subset of 207 sires and maternal grandsires.

Results and Discussion

In analysis 1, fitting AOD classes simultaneously without PA of the 205-d weights of AOD effects resulted in constant estimates of 45 ± 1, 19 ± 1, 6 ± 1, and 19 ± 3 kg for 2, 3, 4, and 11+, respectively, when expressed as deviations from the effect for 5- to 10-yr-old dams. Comparable Hereford TPR adjustments ranged from 27.9 to 23.6 kg for 22- to 26-mo-old dams, 15.9 to 12.7 kg for 34- to 38-mo-old dams, and 7.3 to 5.1 kg for 46- to 50-mo-old dams when adjustments for bull and heifer calves were averaged. The simultaneously estimated AOD effects for 3- and 4-yr-old cows are similar to those reported from this location by Koch and Clark (1955) in a study encompassing a broader array of Hereford genotypes. After applying TPR adjustments to the 205-d weights, reanalysis of the data (analysis 2) resulted in highly significant AOD constant estimates of 20 ± 1, 6 ± 1, 1 ± 1, and 14 ± 3 kg for 2, 3, 4, and 11+, respectively. If the TPR adjustments adequately corrected 205-d weight for AOD effects that are present in this population these constant estimates resulting from analysis 2 would not differ significantly from zero. Their significant departure from zero illustrates an instance of herd × AOD interaction in the Hereford population. The work of Nelsen and Kress (1981) also documented generic herd × AOD interaction effects for Hereford herds participating in the Montana Beef Performance Association. Thus, while TPR adjustments are appropriate to correct for differences in 205-d weight attributable to AOD in the average Hereford herd, they may be inappropriate for individual herds.

To explain the observed departure of AOD effects in the Line 1 population from the Hereford breed norm, a general model for amplified AOD effects under stressful conditions is proposed. Explicitly, the hypothesized model is this: environmental conditions that, from the perspective of the calf, are more limiting to expression of potential for growth from birth to weaning will amplify AOD effects relative to less limiting environmental conditions. The proposed model is consistent with the present results and supported by a variety of studies previously reported.

Inbred animals may be more sensitive to environmental conditions than outbred contemporaries (Falconer, 1989). The preweaning environment at Fort Keogh Livestock and Range Research Laboratory may be more limiting to the expression of growth potential than the average environment in which calves enrolled in the American Hereford Association (1992) Total Performance Records program are raised (John Hough, American Hereford Association, Kansas City, MO, personal communication). DeNise et al. (1988) observed an increasing range of AOD effects for Hereford cattle associated with increasing environmental severity between years in a Southwestern range environment. Anderson and Wilham (1978) and Northcutt et al. (1992) also observed a diminished range of AOD effects with creep feeding. This latter observation is also consistent with the difference in American Hereford Association (1992) AOD adjustments for calves either fed or not fed creep.

Recognizing that inbreeding of dam effects on preweaning growth are environmental to her calf in a manner analogous to other maternal effects was key to consolidating the previously cited results into the hypothesis that as potential for preweaning growth increasingly exceeds environmental adequacy, AOD effects become larger.

Also, inbreeding has resulted in delayed attainment of sexual maturity and mature size in cattle (Nelson and Lush, 1950; Davenport et al., 1965). Thus, young inbred dams may be less physiologically mature, and as a consequence may produce less milk than non-inbred dams of the same chronological age. Cundiff et al. (1974) observed a parallel situation in analyses of data from straightbred and crossbred cows. Adjustments needed to correct weaning weight records from more homozygous straightbred dams to a mature equivalent basis were greater than those required to correct records from more heterozygous crossbred dams.

Delayed maturation associated with inbreeding might be anticipated to result in an interaction between AOD and level of inbreeding in the present study. However, in preliminary analyses of these data such interaction effects were not detected. Since 1972, when 2-yr-old heifers were first calved in Line 1, the intra-contemporary group standard deviation for percentage inbreeding of dams has averaged only approximately 2.8%. Coupled with the colinearity of inbreeding of calf and inbreeding of dam ($r = .83$) this limits the opportunity to detect differential maternal inbreeding effects within AOD subclasses. No line-of-cow × AOD interaction effects were detected in an earlier independent evaluation of contemporary inbred and non-inbred lines of Hereford females producing outcross calves at Clay Center, Nebraska (MacNeil et al., 1989). There may be a further concern regarding confounding of AOD and inbreeding of dam within contemporary groups. Although the tendency for younger dams to be more highly inbred existed in these data ($r = -.19$), this small degree of confounding did not seem problematic to estimation of the effects.

It is granted that causal components of the amplified AOD effects observed have not been conclusively established in this study. Whether inbreeding of the dam and(or) the harsh range environment provide the underlying mechanism for environmentally limited expression of growth potential of the calf, the end result under the proposed model would be amplification of AOD effects relative to breed average. The influence of these amplified AOD effects on genetic predictions was of greater concern in this study than the straightforward observation of the effects themselves.

Comparative statistics quantifying effects of inaccurate PA for AOD on predicted BV are shown in Table 1. The change from PA (analysis 3) to SA adjustment (analysis 1) had more impact on prediction of BV_m for 205-d weight than on BV_d. The very high correlations between BV_d from analyses 1 and 3 indicate that any reranking of direct effects was relatively minor. Correlations between BV_m are expected to be of smaller magnitude than corresponding correlations between BV_d, if the accuracy of genetic evaluation for maternal effects is less than for direct effects. However, the accuracies of genetic evaluations for direct and maternal weaning weight in the Line 1 Hereford population at Miles City were similar in these data. Thus, the observed reranking of maternal BV seems important both for all animals with records and for the subset containing only sires and maternal grandsires. The lack of consistency between analyses in identifying individuals in the central decile is important. Of individuals with BV in the central decile of analysis 1, 68% were in the third and fourth deciles of individuals as ranked for maternal genetic effects by analysis 3. However, dissimilarity of extreme deciles from evaluations using PA and SA for age of

Table 1. Relationships of breeding values (BV) from analyses with simultaneous adjustment for age of dam and analyses with preadjustment for age of dam using Total Performance Records (TPR) procedures

	Sires and maternal grandsires (n = 207)		Animals with records (n = 4,998)	
Statistic	Direct BV	Maternal BV	Direct BV	Maternal BV
Correlation				
Pearson	.97	.84	.98	.87
Spearman	.97	.72	.98	.77
Change in rank				
Average	10.8 ± .6	36.5 ± 1.8	215 ± 3	725 ± 9
Maximum	51	100	1,985	3,085
Percentage of members in intersection of selected subsets[a]				
First decile	75	40	76.8	53.9
Central decile	24	19	53.2	6.6
Last decile	85	80	90.2	90.2

[a]The first decile contains the 10% of individuals with the highest breeding value (BV), the central decile contains the 10% of individuals with BV nearest the mean BV, and the last decile contains the 10% of individuals with the lowest BV.

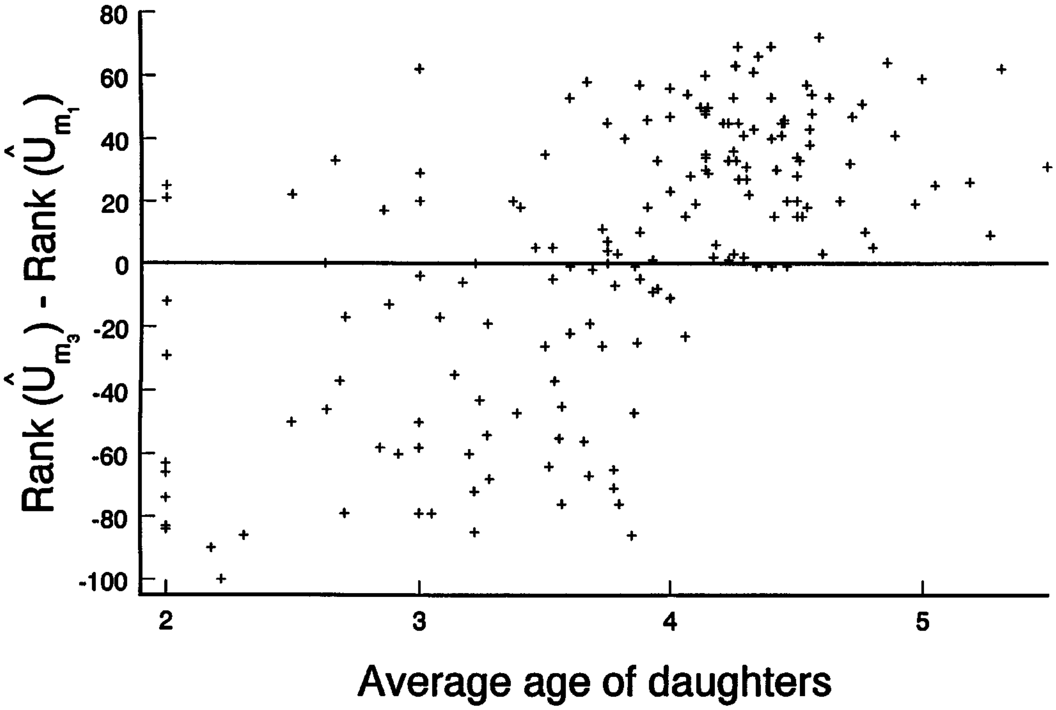

Figure 1. Change in ranking of sires for maternal breeding value from analysis with preadjustment for age of dam (Rank [$\hat{U}_{m_3}$) to analysis with simultaneous adjustment for age of dam [Rank ($\hat{U}_{m_1}$)] given the average age of their daughters upon producing weaning records considered in the analyses.

dam potentially has serious ramifications in selection for milk production.

Presented in Figure 1 is the relationship of change in rank of maternal BV from analysis 3 to analysis 1 for the 207 sires and maternal grandsires with the average age of their daughters. Sires whose daughters had the opportunity to produce progeny to a more advanced age were over-evaluated relative to sires whose daughters had relatively few years in production. In these data, two circumstances contribute to the impact of this effect on genetic evaluation and the prediction of genetic trend. Perhaps somewhat unique to the present data, calving 2-yr-old heifers commenced in 1972. Thus, the potential for systematic error associated with their records when preadjusted for age of dam only exists in the data from then on. However, recently used sires have only young daughters and sires whose predicted BV_m for 205-d weight depended disproportionately on information from younger daughters were under-evaluated based on records using PA for AOD relative to their evaluation with SA for AOD.

A further result of this systematic error in genetic evaluation was alteration of predicted genetic trend. Plotted in Figure 2 are predicted trends in BV_d and BV_m from analyses 1 and 3. Departures of the direct and maternal genetic trends both occurred coincident with the initiation of two-year-old calving in this herd. Beginning in the mid-1970s, there was a downward shift of the trend in BV_d when 205-d weights were preadjusted for AOD compared to when they were simultaneously adjusted. This shift most likely results from a change in the mean that resulted from initiation of 2-yr-old calving and under-correction for the corresponding AOD effect using industry-standard adjustment procedures. A more pronounced difference in trends of BV_m was also observed. With PA for AOD effects using industry-standard methods trend in BV_m for 205-d weight was essentially nil or slightly negative. However, with SA for AOD the predicted genetic trend continued to increase. Bonaïti et al. (1993) also observed biased prediction of genetic trend for milk production in dairy cattle resulting from inaccurate PA for age or parity effects.

Presented in Table 2 are results from simulations to determine correlations of predicted BV with simulated true values. For BV_d, any systematic error introduced by differences in procedures used to adjust for AOD were minor. Differences in correlations between true and estimated BV_d were less than .02 whether PA or SA was used to account for the AOD effects. However, corresponding correlations between BV_m were .13 to .17 less when AOD effects were accounted for by PA rather than SA. This loss of precision in genetic evaluation seems too large to ignore. Because both PA and SA represented approximations of the model used to simulate data, calculated accuracy consistently overestimated the correlation between predicted and true BV. Again, overestimation was most pronounced when 205-d weight was preadjusted for AOD.

Table 2. Accuracies and average correlations between simulated and predicted breeding values for 205-day weight resulting from analyses with either simultaneous (SA) or preadjustment (PA) for age of dam effects

	Direct breeding value		Maternal breeding value	
Item	SA	PA	SA	PA
Animals with records				
Correlation	.516 ± .004	.507 ± .005	.511 ± .004	.385 ± .007
Accuracy	.538 ± .004	.538 ± .001	.570 ± .001	.575 ± .001
Sires and maternal grandsires				
Correlation	.659 ± .004	.644 ± .005	.597 ± .006	.429 ± .009
Accuracy	.626 ± .007	.627 ± .007	.628 ± .006	.635 ± .006

The naturally occurring pyramid structure revealed by herd- and flock-book analyses in many pedigreed breeds of livestock (Robertson, 1953) has positioned Miles City Line 1 as a nucleus breeding herd within the Hereford breed. Dickenson (1984) estimated that Miles City Line 1 ancestry appeared in the pedigree of over two-thirds of registered Hereford cattle. Dissemination of Line 1 germ plasm from Fort Keogh Livestock and Range Research Laboratory continues with annual sales of bulls and surplus females, although the exact contribution to the current generation of Hereford cattle is unknown. To the extent that Line 1 germ plasm is disseminated to the Hereford breed, genetic improvement throughout that breed is conditioned on the genetic improvement in the nucleus (Bichard, 1971). It is in this context that genetic evaluation free of systematic error in Line 1 is particularly important. Breed-wide genetic evaluation has unquestioned advantages in accelerating genetic improvement over within-herd mass selection (Hough et al., 1985). The advantages of breed-wide evaluations are reduced when systematic error is introduced by inappropriate adjustment for fixed effects. Further, it is unlikely that these results are unique to the Line 1 situation, because there are other seedstock herds making important contributions to Hereford and other breeds. Certainly, the AOD effects in some of these other nucleus herds also are not representative of the breed average.

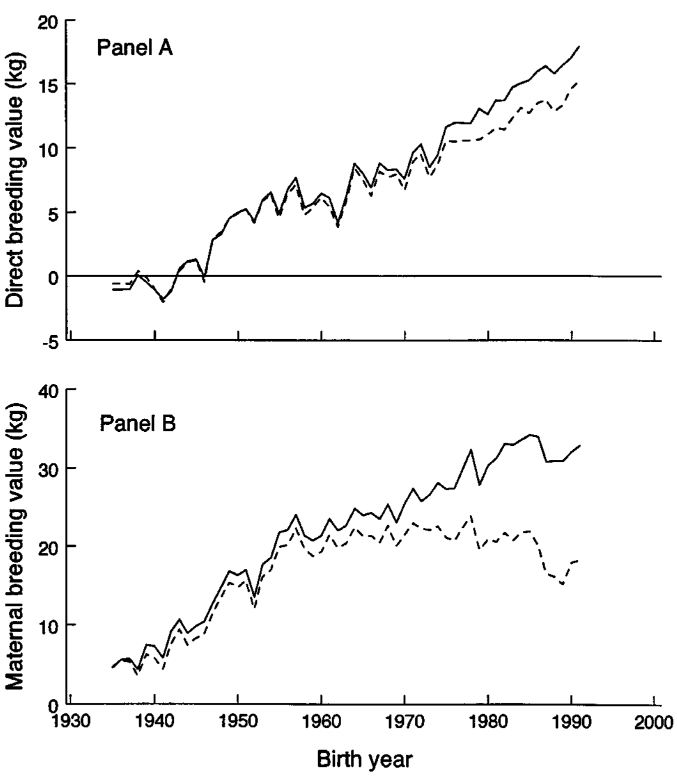

Figure 2. Effects of simultaneous adjustment (solid line) vs preadjustment (dashed line) for age-of-dam on trends in direct (panel A) and maternal (panel B) breeding values for 205-d weight.

Implications

Further investigation toward accounting for herd-specific effects in genetic evaluation schemes seems appropriate. One approach may be to more narrowly define contemporary groups, even at the expense of reduced numbers of animals within those groups. Other alternatives would include Baysian approaches using breed-wide adjustments as priors or random regressions on age of dam (AOD) specific to each herd. Understanding the dependance of AOD effects on level of inbreeding and(or) environmental severity also requires more study.

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