

Review

National genetic improvement programmes in the United States beef industry

L.L. Benyshek* and J.K. Bertrand

The University of Georgia, Athens, Georgia 30602, United States

Received 21 February 1989; accepted 4 October 1989

There are at least 15 breeds of beef cattle in the United States which have or are in the process of developing national genetic evaluation programmes. These 15 breeds represent over 600 000 new registrations each year. The commercial cattle industry is accepting, in fact, demanding estimates of genetic values on yearling bulls. Single and multiple analyses are being conducted depending on the breeds and traits evaluated. Models account for maternal ability for those traits maternally influenced; however, the major emphasis is on growth. There is considerable interest in developing evaluations for carcass characteristics. Generally, the theory of mixed linear models for genetic evaluation is finding widespread application in the United States beef cattle industry.

Daar is ten minste 15 vleisbeesrasse in die Verenigde State wat gebruik maak van nasionale genetiese evaluasieprogramme of in die proses is om sulke programme te ontwikkel. Hierdie 15 rasse verteenwoordig meer as 600 000 nuwe registrasies elke jaar. Die kommersiële beesbedryf aanvaar en dring selfs aan op beramings van genetiese waardes van jaaroud-bulle. Enkel- en meervoudige analyses word uitgevoer afhangende van die ras en die eienskap wat geëvalueer word. Die modelle neem materne vermoë in ag vir kenmerke wat maternaal beïnvloed word, alhoewel die meeste klem op groei geplaas word. Daar is heelwat belangstelling in die ontwikkeling van evaluasies vir karkaseienskappe. Die teorie van gemengde lineêre modelle vir genetiese evaluasie is besig om algemeen inslag te vind in die vleisbeesbedryf van die Verenigde State.

Keywords: Beef cattle, genetic evaluation, mixed model methodology.

* To whom correspondence should be addressed.

The selection process as defined by Wright (1969) is one that alters the frequency of genes affecting a particular characteristic in a directed fashion without change of the genetic material (mutation) or introduction from outside the population (immigration). Population genetic change is difficult for breeders to understand because they deal with individuals in making selection decisions and in their merchandising programmes. Nevertheless, those breeds (populations) which practice intense selection for characteristics of economic importance to the cattle industry will change genetically and eventually be the successful populations because they will leave the most progeny in the next generation. The genetic improvement of a population (breed) can not overlook the individual because the individual, if selected, is the vehicle containing the genes which are to be passed on to the next generation. Bull selection is central to directed changes in gene frequency of any defined beef cattle population because of the low reproductive rate in beef females. Sophisticated genetic prediction techniques have been developed in the United States to help beef cattle producers make sound selection decisions.

History of genetic prediction in the United States

Benyshek (1986) and Benyshek, Johnson, Little, Bertrand & Kriese (1988) discussed historically the development of the US national genetic improvement programmes. The chronology of US beef cattle performance testing (Baker, 1967; 1975) on which genetic prediction is based, began in the 1930s with research initiated at the US Range Livestock Research Station, Miles City, Montana. Research continued through the 1940s with large regional programmes (W-1,

NC-1 and S-10) and the first bull test stations appeared. In the late 1940s and early 1950s, beef cattle improvement (BCI) programmes began in several states (California, New Mexico and Montana). In 1955 the first Beef Cattle Improvement Association (BCIA) was founded in Virginia and Performance Registry International was initiated. In 1959, beef cattle breed registry associations began to formalize the collection of records by their members. In the 1960s, performance programmes were nurtured and began to flourish providing sound objective information which breeders could use in making selection decisions. In 1968 an extraordinary event occurred with the formation of the Beef Improvement Federation (BIF). BIF began to provide the framework for standardized and systematic procedures which the beef cattle performance movement so desperately needed.

One of the working committees established within BIF during that first meeting, was to address National Sire Evaluation (NSE). Drawing on the experiences of the dairy industry, guidelines were approved by the BIF board in 1971 and published in 1972. In 1971—72 the American Simmentaler Association published the first National Sire Summary. Only a few far ranging thinkers understood what the publication of this document really meant to the beef industry. Bulls were now compared across herds and/or generations. Beef cattle breeding had entered the twentieth century!

Dr C.R. Henderson presented an invited paper at the 1972 American Society of Animal Science meetings which formalized his mixed model procedures providing best linear unbiased predictions (BLUP) of breeding value.

Willham (1972) discussed the concept of breeding value at a BIF regional meeting held in Montgomery, Alabama. He outlined a procedure for estimating breeding values which was to become a corner-stone in the structure of beef cattle improvement programmes. The procedure provided estimated breeding values (EBVs) at the same time that within herd performance summaries were being computed. The EBV concept was soon adopted by the Angus, Hereford, Polled Hereford and Simmentaler breeds.

The increased use of artificial insemination in beef cattle has provided a data structure which lends itself to rather sophisticated models. The increased sophistication of mathematical models used in NSE has paralleled the improvements in computer hardware. The introduction of large-scale scientific 'super' computers has certainly opened the door to applications of models not thought possible only a few years ago.

National Sire Evaluation procedures first used rather basic models including contemporary group effects, sire effects and random error. The sire effects become the 'Expected Progeny Differences' (EPDs) when the model is applied. The model required that sires and contemporary groups be 'connected', that is at least some sires must be used over more than one contemporary group thereby forming 'ties' between sires and contemporary groups. Each contemporary group had to have at least two sires represented. The model assumed that sires had been mated to comparable sets of cows (cows randomly allotted to sires) and that progeny were treated similarly within contemporary groups. The model assumed genetic trend was non-existent or relatively unimportant in the population. These were essentially safe assumptions in the early 1970s for analyses of field data from the newly imported Continental breeds. The early designed programmes implemented by the domestic British breeds were structured to meet these assumptions. The analyses procedures of the early 1970s approximated the true mixed model procedures described by Henderson (1973). The BLUP procedures as described by Henderson with this basic model were fully implemented in the analyses of the designed sire evaluation programmes of the British breeds (Angus, Hereford, Polled Hereford and Shorthorn, 1974—77) and in the 1976 Limousin field data analysis.

In the decade from 1975 to 1985, mathematical models used in the analyses began to account for more and more of the factors which could possibly bias the EPDs. Henderson (1973) discussed the use of the inverse of Wright's Numerator Relationship matrix to enhance the accuracy of genetic prediction. The relationship matrix provided the means to incorporate pedigree information in the analysis procedure and a method to account for genetic trend. However, taking the inverse of this matrix seemed computationally infeasible at that time. Henderson (1975) published a paper concerned with a rapid method for computing the inverse of a relationship matrix. This opened the door to one of the major improvements in mathematical models used for sire evaluation. This improvement was not incorporated immediately, but by 1983 the Limousin and Red Angus analyses had incorporated relationships among sires. In 1984, Angus, Polled Hereford and Hereford began using the relationship matrix. The use of the A-inverse, as it is now referred to,

certainly was a major breakthrough in NSE because pedigree breeding now began to take on real meaning.

Even with the improvements in models, breeders and researchers alike continued to question the effect of specific matings on sire evaluation results. At the same time (late 70s and early 80s) computer hardware was improving at a phenomenal rate. By 1984, it seemed feasible to include a dam effect in the basic model for sire evaluation. This was accomplished in the 1984 summaries for Hereford, Angus and Limousin breeds. In 1984, model dependency on difficult to verify assumptions was becoming less and less a problem in sire evaluation. The incorporation of dams into the model along with the A-inverse provided breeders the most accurate prediction of breeding values to date.

Another problem which continued to burden breeders and researchers alike was the older age at which bulls were entering national sire summaries. Scientists were concerned about an increase in the generation interval due to the increased use of older sire summary bulls which would cause reduced genetic change per year. Another important consideration was that many breeders like to use young bulls; therefore, they were making selection decisions based on information other than that contained in sire summaries.

Most researchers had contended that NSE was a means to an end rather than the ultimate in genetic improvement of performance characteristics. It was generally recognized that unless NSE was somehow merged with on-farm and ranch testing programmes, genetic progress would be slow particularly in the commercial industry (Willham, 1979; 1982).

Henderson & Quaas (1975) discussed methods for best linear unbiased prediction of breeding values utilizing records on large numbers of relatives as well as the individual's own record. The procedures were further discussed and developed in papers by Quaas & Pollak (1980) and Pollak & Quaas (1981). The mathematical model, termed the 'animal model' by these researchers, was less dependent on hard-to-verify assumptions, and it incorporated the sire's own record into the analysis. It also provided genetic values on dams and young animals not yet producing progeny. The procedure adjusted for the merit of the mates of the individual reducing substantially, if not totally eliminating the effects of non-random mating. Finally, the procedure provided simultaneous breeding values (or EPDs) for direct growth and maternal ability for those traits which are maternally influenced.

The 'animal model', along with the data structure the purebred beef industry, had established by ten years of AI and NSE seemed to provide the ultimate in genetic prediction techniques for beef cattle – across herd and/or generation evaluations of all individuals (male and female) in the breed. However, the complexity of the model resulted in a computational nightmare. In the 1980 paper by Quaas & Pollak, an equivalent model, the reduced animal model, was also discussed. The reduced animal model was less of a computational nightmare but also seemed beyond computing strategy and hardware of the time.

In 1983 a workshop sponsored by Winrock International, concerning the prediction of genetic values for beef cattle, laid the groundwork for the next improvements in prediction of breeding values. The availability of large scale scientific

computers and the experience gained in developing computing strategy for the sire-dam model in 1983—84, was encouraging with respect to the application of the reduced animal model. In late 1984, the model was applied in the Limousin and Brangus breeds. This technology has now been adopted by nearly all the major beef breeds in the United States.

The technology in prediction of genetic values is rapidly being adopted across the US beef cattle industry, because now the commercial industry can share directly and much earlier in the purebred industry genetic progress. Young bulls not yet producing progeny, now have genetic values (EPDs) comparable across herds and/or generations just as the older progeny tested sires have had for years in NSE. In 1985, the purebred cattle industry moved from National Sire Evaluation to National Cattle Evaluation.

Current mixed model methodology used in the US beef industry

The following is a brief introduction to the National Cattle Evaluation methodology used in the United States.

The factors affecting weaning mass, which is a maternally influenced trait in beef cattle, can be outlined as follows:

- I. Genes received from the individual's sire.
- II. Genes received from the individual's dam.
- III. Milking ability of the individual's dam.
 - A. Dam's genotype for milk.
 - 1. Genes received from her sire for milking ability (maternal grandsire of the individual).
 - 2. Genes received from her dam for milking ability (maternal granddam of the individual).
 - B. Permanent environmental factors affecting the dam's milking ability (e.g. loss of a quarter to mastitis).
- IV. Fixed factors.
 - A. Contemporary group environment (groups are defined as animals of similar age, same breed, same sex, given equal opportunity to perform; i.e. same management, same year, etc.).
 - B. Age of calf, adjusted to 205 days of age prior to analysis.
 - C. Age of dam, additive adjustment prior to analysis.
 - D. Others, may be unknown or considered part of the contemporary group.

A model accounting for the factors in the above outline is:

Record of the individual	Fixed = contemporary group effect	Breeding value + of the individual	Maternal breeding value + of the dam	Permanent environment + affecting the dam	error
--------------------------	-----------------------------------	------------------------------------	--------------------------------------	---	-------

In matrix notation the model is:

$$Y = Xb + Z_d u_d + Z_m u_m + Z_{pe} u_{pe} + e$$

where X and Z are incidence matrices relating the fixed effects, b, and the random factors (u_d , direct breeding value; u_m , maternal breeding value; and u_{pe} , permanent environment) to the vector of records Y.

The variance-covariance matrix for the random effects in the model is:

$$V \begin{pmatrix} u_d \\ u_m \\ u_{pe} \\ e \end{pmatrix} = \begin{pmatrix} g_{11}A & g_{12}A & O & O \\ & g_{22}A & O & O \\ & & \text{Symmetric} & g_{33}I \\ & & & \sigma_e^2 I \end{pmatrix}$$

where

- A = Wright's Numerator Relationship matrix,
- g_{11} = additive genetic variance direct, σ_a^2 ;
- g_{22} = additive genetic variance maternal, σ_m^2 ;
- g_{12} = additive genetic covariance between direct and maternal, $\sigma_{a,m}$ and
- $g_{33} = \sigma_{pe}^2$.
- I = identity matrix.

The following occurs because u_d and u_m represent the same animal:

$$V \begin{pmatrix} u_d \\ u_m \end{pmatrix} = \begin{pmatrix} g_{11} & g_{12} \\ g_{12} & g_{22} \end{pmatrix} \otimes A = G_o \otimes A$$

where \otimes means direct product. Therefore:

$$(G_o \otimes A)^{-1} = G_o^{-1} \otimes A^{-1}$$

Taking the inverse of G_o and post multiplying by σ_e^2 gives the following:

$$\begin{pmatrix} \alpha_1 & \alpha_2 \\ \alpha_2 & \alpha_3 \end{pmatrix} = \begin{pmatrix} \sigma_a^2 & \sigma_{a,m} \\ \sigma_{a,m} & \sigma_m^2 \end{pmatrix}^{-1} \sigma_e^2 = G_o^{-1} * \sigma_e^2$$

and the mixed model equations for a maternally influenced trait become:

$$\begin{pmatrix} X'X & X'Z_d & X'Z_m & X'Z_{pe} \\ Z'_d Z_d + A^{-1} \alpha_1 & Z'_d Z_m + A^{-1} \alpha_2 & Z'_d Z_{pe} \\ & Z'_m Z_m + A^{-1} \alpha_3 & Z'_m Z_{pe} \\ & & Z'_{pe} Z_{pe} + I \alpha_4 \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{u}_d \\ \hat{u}_m \\ \hat{u}_{pe} \end{pmatrix} = \begin{pmatrix} X'Y \\ Z'_d Y \\ Z'_m Y \\ Z'_{pe} Y \end{pmatrix}$$

where $\alpha_1 = \sigma_e^2 * g^{11}$, $\alpha_2 = \sigma_e^2 * g^{12}$, $\alpha_3 = \sigma_e^2 * g^{22}$, and $\alpha_4 = \sigma_e^2 / \sigma_{pe}^2$.

The prediction of direct breeding value for the i^{th} animal is:

$$\hat{u}_{di} = \left(\frac{1}{Z_{ii} + a^{ii} \alpha_1} \right) (Y - \hat{b}_i - \hat{u}_{m_{dam}} - \hat{u}_{pe_{dam}}) - \left(\frac{1}{Z_{ii} + a^{ii} \alpha_1} \right) \left(\sum_{j \neq i} a^{ij} \alpha_1 \hat{u}_{dj} \right) - \left(\frac{1}{Z_{ii} + a^{ii} \alpha_1} \right) \left(\sum_j a^{ij} \alpha_2 \hat{u}_{mj} \right)$$

where

$Y - \hat{b}_i - \hat{u}_{m_{dam}} - \hat{u}_{pe_{dam}}$ represents the contribution of the individual's own record;
 $\sum_{j \neq i} a^{ij} \alpha_1 \hat{u}_{dj}$ is the contribution of the individual's relatives and adjustment for mates;
 $\sum_j a^{ij} \alpha_2 \hat{u}_{mj}$ is the adjustment of the individual's direct breeding value for the relationship between growth and milk.

The prediction of maternal breeding value for the i^{th} individual is:

$$u_{mi} = \left(\frac{1}{k + a^{ii}\alpha_3} \right) \left(\sum_k Y_k - Xb_1 - \hat{u}_k - \hat{u}_{pe,dam} \right) - \left(\frac{1}{k + a^{ii}\alpha_3} \right) \left(\sum_{j \neq i} a^{ij}\alpha_3 \hat{u}_{mj} \right) - \left(\frac{1}{k + a^{ii}\alpha_3} \right) \left(\sum_j a^{ij}\alpha_2 \hat{u}_j \right)$$

The first line in the case of a female represents the contribution of the calves' records taken as a trait of the dam (her calves' weaning weights indicate her milking ability). The second line represents relative's contribution and the last line adjusts for the relationship between milk and growth.

The animal model equations for a maternally influenced trait can be reduced in number as shown by Quaas & Pollak (1980). A discussion is given by Bertrand *et al.* (1985) of how to build the reduced animal model (RAM) equations for a maternally influenced trait. The RAM equations which represent only the parents in the population are given in the matrices of Scheme 1.

Back-solutions for non-parents in the population are given by:

$$\hat{u}_{di} = \frac{1}{1 + \alpha_{11}D_i^{-1}} \left(Y_i - \hat{b}_i - \hat{u}_{m,dam} - \hat{u}_{pe,dam} - \frac{1}{2}\hat{u}_{d,sire} - \frac{1}{2}\hat{u}_{d,dam} \right)$$

and

$$\hat{u}_{mi} = \frac{1}{2}\hat{u}_{m,sire} + \frac{1}{2}\hat{u}_{m,dam} + \frac{\alpha_{11}}{\alpha_{12}} \left(\hat{u}_{di} - \frac{1}{2}\hat{u}_{d,sire} - \frac{1}{2}\hat{u}_{d,dam} \right)$$

where \hat{u}_{di} is direct breeding value for growth and \hat{u}_{mi} is maternal breeding value. The value of $\alpha_{11} = \sigma_c^2 / \sigma_a^2$, $\alpha_{12} = \sigma_c^2 / \sigma_{a,m}$ and the value of $D = 1/2$ or $3/4$.

An accuracy value is computed for each EPD that is in a sire summary. Accuracy in NCE programmes is described by the following expression:

$$1 - \sqrt{\frac{\text{Prediction error variance}}{\text{Genetic variance}}}$$

The prediction error variance (PEV) must be approximated because obtaining the true PEV requires that the diagonal elements of the inverse coefficient matrix for RAM be computed. Some approximation strategies that could be used require that contemporary groups be absorbed into the sire and dam portions of the additive and maternal sections of RAM. Next, A-inverse is added to the absorbed equations. Some possible approximations that can be produced for individual 'i' from these sire and dam equations are:

1. $1/d_{ii}$ where d_{ii} represents a diagonal element from the absorbed equations.
2. $1/d_{ii} + (1/d_{ii})^2 \left(\sum_{j \neq i} d_{ij}^2 / d_{jj} \right)$ where d_{ij} represents an off-diagonal element.
3. $c_{ii}^{-1} + c_{ii}^{-1} \left(\sum_{j \neq i} c_{ij} c_{jj}^{-1} c_{ji} \right) c_{ii}^{-1}$ where c_{ii} , c_{ij} , and c_{ji} represent blocks of elements from the absorbed equations.

The accuracy of the approximations favours 3 over 2 over 1, but the ease of computing favours 1 over 2 over 3. The decision of which to use depends on the computing facilities, the size of the matrix and the computing time available.

The accuracies for non-parents can then be computed as a linear combination of the parental accuracies. Discussions of approximations for PEV are given by Greenhalgh, Quaas & Vleck (1986) and Benyshek *et al.* (1988).

The application of the reduced animal model solves many problems in the prediction of genetic values; however, for maximum benefit it requires a multiple trait analysis. That is, the analysis of two or more traits simultaneously. Multiple trait mixed model analysis considers the relationship between two or more traits to enhance the accuracy of prediction. The use of multiple trait analyses can correct for selection bias such as occurs in beef cattle data when some individuals are culled prior to a test period. An example is the effect of selection at weaning on post-weaning gain test. Research with the Simmentaler and Gelbvieh breeds resulted in sire

Scheme 1

Symmetric	$\begin{matrix} X'_p X_p + X'_n R^{22} X_n & X'_p + \frac{1}{2} X'_n R^{22} P \\ Z'_p Z_p + \frac{1}{4} P' R^{22} P + A_{p,p}^{-1} \alpha_1 & Z'_p Z_p + \frac{1}{2} P' R^{22} Z_{mp} + A_{p,p}^{-1} \alpha_2 \end{matrix}$	$\begin{matrix} X'_p Z_{mp} + X'_n R^{22} Z_{mp} \\ Z'_{mp} Z_{mp} + Z'_{mp} R^{22} Z_{mp} + A_{p,p}^{-1} \alpha_3 \end{matrix}$	$\begin{matrix} X'_p Z_{pe} + X'_n R^{22} Z_{pe} \\ Z'_p Z_{pe} + \frac{1}{2} P' R^{22} Z_{pe} \\ Z'_{mp} Z_{pe} + Z'_{mp} R^{22} Z_{pe} \\ Z'_{pe} Z_p + Z'_{pe} R^{22} Z_{pe} + I \alpha_4 \end{matrix}$
-----------	---	--	--

x	$\begin{matrix} \hat{b} \\ \hat{u}_d \\ \hat{u}_m \\ \hat{u}_{pe} \end{matrix} \text{ parents}$	=	$\begin{matrix} X'_p Y_p + X'_n R^{22} Y_n \\ Y_p + \frac{1}{2} P' R^{22} Y_n \\ Z'_{mp} Y_p + Z'_{mp} R^{22} Z_{mp}^* Y_n \\ Z'_{pe} Y_p + Z'_{pe} R^{22} Z_{pe}^* Y_n \end{matrix}$	<p>* Indicates Z matrices relating non-parent records to parents' maternal breeding values or permanent environment effect.</p>
---	---	---	---	---

where R^{22} is defined as

$$\begin{matrix} \frac{1}{1 + D\alpha_1^{-1}} \\ \frac{1}{1 + D\alpha_1^{-1}} \end{matrix}$$

The value of D is 1/2 or 3/4 depending on whether one or both parents are known. The α values are as previously defined.

summaries in 1986 for those breeds based on multiple trait analyses. The Gelbvieh analysis uses the reduced animal model while the Simmentaler uses a sire-maternal grandsire model (latter provides the same values for sires as the reduced animal model). In 1987, the Limousin and Brangus Sire Summaries began using a multiple trait analysis. In 1988, almost all breeds have incorporated a multiple trait analysis into their national evaluation procedures.

The development of technology for genetic prediction has been indeed astounding. Discussion of the current technology used in the beef industry is given by Benyshek (1987) and Benyshek *et al.* (1988).

Evidence that genetic predictions can impact breeding programmes

The procedures used in making genetic predictions have been developed on a sound theoretical basis. Genetic theory has always been difficult to directly substantiate and has relied many times on indirect proof. Research efforts must be enhanced to challenge the theory and assumptions on which national beef cattle genetic improvement programmes are based.

Perhaps the first place to look for evidence that sire evaluation is influencing breeding programmes is the genetic trend in breeds which have been using such programmes. Genetic trends are obtained by averaging breeding values by birth year and then regressing those averages on time (years).

Angus and Hereford weaning mass trends for 1971–1985 are 0,96 and 1,29 kg/year, respectively. Yearling mass trends for Angus and Hereford are 1,87 and 2,23 kg/year, respectively. The trends are probably not significantly different between these breeds.

The number of bulls evaluated through National Sire Evaluation became significant in the late 70s for the two breeds. The rate of genetic change for weaning and yearling mass from 1978 to 1985 is almost double the rate for the period 1971 to 1978. The magnitude of the effect of NSE on these breeds is difficult to quantitate; however, there has been increased interest in performance and along with that interest, has come greater use of outstanding sire summary bulls in both breeds.

Milking ability has changed in the Hereford breed over the years, however, the Angus breed has not made any change in this trait. This difference between the breeds probably results from the fact that Hereford breeders have been more conscientious of milking ability since that breed is generally thought to produce less milk than the Angus breed. Both breeds now have access to milking ability EPDs through their National Cattle Evaluation (NCE) programmes so that genetic change can be made rapidly for that trait. Breeders need to be cautious not to over-emphasize milking ability in their selection programmes since some environments will not support an over abundance of milk in the beef cow.

Birth mass has changed in both breeds. This change is a correlated response to selection for growth and frame. It is impossible to determine the practical significance of these birth mass changes. It is safe to say that birth mass extremes are a problem for the industry because of their effect on calving ease. In the United States, birth mass effects on calving ease are most important in heifers. A majority of

calving difficulty problems could be eliminated by selection of easier calving bulls to use on heifers. Information is available through the NCE programmes to help identify bulls which produce calves with smaller birth masses.

In the spring breeding season of 1977, a project was initiated at the Northwest Georgia Branch Experiment Station (NWBS), Calhoun, Georgia, to determine the magnitude of genetic change for single trait (yearling mass) selection. The selection practiced in this herd was through NSE, that is bulls used in the selection line were the top yearling mass EPD bulls from the American Hereford Association Sire Evaluation programme. A control line was maintained to quantitate environmental changes in the project. Genetic trends for several traits of economic importance were obtained by regressing differences between the selection line and the control line on years. Most of the genetic change was due to sire selection since little selection was practiced on the heifer replacements going into the selection line. Hough, Benyshek & Mabry (1985) summarized the study.

Differences between the selection line and control line are shown in Table 1. Observation of the yearling mass differences in Table 1 show a linear increase from 13,6 kg in 1978 to 43,2 kg in 1983. This represents genetic change of 6,4 kg/year. This is at least double the trend shown in the industry at present. Obviously part of the difference between industry change and genetic change in this research project is due to the single trait selection practiced. Single trait selection is seldom the situation in a beef breeding programme; however, the project does show that rapid genetic change can be made in a beef cattle herd.

Observation of the differences in Table 1 between lines for other traits gives an indication of the response of traits correlated with yearling mass to the intense selection for yearling mass. Generally, the correlated responses have been favourable. Birth mass has increased; however, this increase did not affect calving ease as dramatically as expected. Perhaps of some concern was the small change in post-weaning average daily gain. Much of the change in yearling mass seems to be coming through weaning mass. This result may point to the need for a multiple trait analysis which would more accurately account for the effects of selection at weaning on yearling mass (many records are lost between weaning and yearling). The project has not addressed changes in fertility; however, it is encouraging to see only small changes in calving difficulty and positive changes for scrotal circumference and pelvic size.

Generally, the trend in the NWBS herd had been at least twice that in the Hereford breed until 1985. The use of low birth mass EPD bulls with lower yearling mass EPDs on a large number of heifers appears to have contributed to some decline in the rate of genetic change in the NWBS herd. Basically, this decline in the rate of genetic change from 1984 to 1985 indicates the necessity of maintaining intense selection pressure if rapid genetic improvement is to be accomplished. If calving difficulty becomes a problem as it did in the 1984 calf crop then it is imperative to find bulls with low birth mass EPDs which can also continue changing post-natal growth. It is of interest that calving difficulty was not a problem in the first six calf crops at the NWBS (see Table 1).

Table 1 Differences^a between the selection line and control line

Trait	Years						Genetic change year ^c
	1978	1979	1980	1981	1982	1983	
Birth mass (kg)	1,5	1,6	1,3	1,8	0,7	3,1	0,3
Calving ease ^b	0,10	-0,13	0,09	0,25	0,13	0,28	0,05
% Live calves within 24 h	-1,1	-0,1	1,5	-4,5	-2,5	-0,1	-0,3
Adjusted weaning mass (kg)	2,7	8,6	7,3	21,8	19,5	30,9	5,0
Post-weaning ADG (g/d)	59,0	63,5	95,3	59,0	59,0	81,6	9,1
Adjusted yearling mass (kg)	13,6	18,6	24,5	30,5	29,5	43,2	6,4
Yearling hip height (cm)	3,5	3,8	4,1	6,1	4,3	5,6	0,8
Yearling fat thickness (cm)	0,05	-0,02	-	-0,02	-0,08	-0,02	0,0
Yearling scrotal circumference (cm)	-	1,0	0,2	1,3	0,8	2,0	0,3
Yearling pelvic area (cm ²)	8	11	13	16	7	13	1,3

Table adapted from Hough *et al.* (1985).

^a Selection line least-squares mean – control line least-squares mean.

^b Score 1 = no assistance; 2 = minor assistance; 3 = major assistance; 4 = Caesarean section; 5 = abnormal presentation.

^c Regression of line differences on years.

In addition to the change in selection pressure, another contribution to the decrease in yearling mass genetic change was that one of the top EPD bulls selected for use in the project, produced progeny which did not perform up to expectation. This may have been due to random chance (simple sampling error) or perhaps a sire by environment (herd) interaction. Even with the decline from 1984 to 1985 the NWBS herd is changing much more rapidly than the Hereford breed.

No attention has been given to maternal (milking ability) EPDs in the selection of bulls for the NWBS. As might be expected for a trait which is not emphasized in the selection procedure, the NWBS milking ability breeding values have been up and down during the study.

Frame size has never been a consideration in the NWBS selection programme. Generally, size (as indicated by hip height) appears to be increasing at a more rapid rate in the NWBS cattle than in the general Hereford population. This change is due to the relationship between mass and height.

The NWBS project shows that rapid genetic change can be accomplished with single trait selection. However, caution must be exhibited since efficient beef cattle production requires the consideration of several economic characteristics. The information now available through National Cattle Evaluation programmes will provide the necessary genetic values to consider several traits in a selection programme. The concept of optimums continues to gather support in the commercial cattle industry. The successful commercial breeder is learning how to sort young bulls on the basis of EPDs from different breeds which can then be put together through crossbreeding to enhance production efficiency.

A question of importance to both commercial and purebred cattle breeders is the reliability of genetic values (EPDs) computed for young animals which have not yet produced progeny. A study concerning this question has been conducted at the University of Georgia with Limousin and Hereford for post-weaning gain (Benyshek *et al.*, 1988). The study involved 71 Limousin and 138 Hereford bulls, all of

which had legitimate individual post-weaning records as well as progeny with records. Expected progeny differences were computed for these bulls using the reduced animal model, first based on their record plus pedigree and secondly based on only their progeny plus pedigree. The Limousin bulls all had between 10 and 30 progeny, whereas the Hereford bulls all had at least 30 progeny. The rank correlations between these two sets of EPDs were found to be 0,59 and 0,58 for Limousin and Hereford, respectively. This is in contrast to correlations for within contemporary group ratios for these bulls and their EPDs based on progeny which were 0,17 and 0,20 for the Limousin and Hereford, respectively. This does not prove conclusively that non-parent EPDs are the best predictors of breeding worth; however, it does show that basing selection decisions on performance ratios may not retain those bulls which will have high EPDs based on progeny. These correlations point out the necessity of accounting for genetic competition in the contemporary group when comparing across herds. This study suggests that the commercial industry can buy young bulls with more confidence that the values on which they select the bulls will indeed turn into more kilograms of product in their herds.

Generally, National Cattle Evaluation has been firmly established in the United States. Theoretically the procedures are sound; however, considerable research needs to be done in refinement of the procedures and more education of producers will be required for maximum success in the industry. Indications are that programmes are working and genetic change is taking place in the cattle industry.

References

- BAKER, F.H., 1967. History and development of beef and dairy performance programs in the United States. *J. Anim. Sci.* 26, 1261.
- BAKER, F.H., 1975. The Beef Improvement Federation. *World Rev. Anim. Prod.* 11: Sept.—Dec.
- BENYSHEK, L.L., 1986. Sire Evaluation – Where we've come from. In: *Proceeding of the Beef Improvement Federation, Animal Meeting and Research Symposium.*

- BENYSHEK, L.L., 1987. Reduced Animal Model predictions and back-solutions: An overview of currently used methodology for genetic prediction. In: Predictions of genetic value for beef cattle. Proceedings of Workshop II, The Beef Improvement Federation. Kansas City, MO.
- BENYSHEK, L.L., JOHNSON, M.H., LITTLE, D.E., BERTRAND, J.K. & KRIESE, L.A., 1988. Applications of an animal model in the United States beef cattle industry. In: Proceedings of the Animal Model Workshop. *J. Dairy Sci.* 71, Suppl. 2.
- BERTRAND, J.K., BENYSHEK, L.L. & LITTLE, D.E., 1985. The reduced animal model equations for national cattle evaluation. In: Proceedings Beef Improvement Federation Meetings. Madison, WI. p. 149.
- GREENHALGH, S.A., QUAAS, R.L. & VAN VLECK, L.D., 1986. Approximating prediction error variances for multiple trait sire evaluations. *J. Dairy Sci.* 69, 2877.
- HENDERSON, C.R., 1973. Sire evaluation and genetic trends. In: Proceedings Anim. Breed. and Genet. Symp. in honor of Dr. Jay L. Lush. *Am. Soc. Anim. Sci.*, Champaign.
- HENDERSON, C.R., 1975. Rapid method for computing the inverse of a relationship matrix. *J. Dairy Sci.* 58, 1727.
- HENDERSON, C.R. & QUAAS, R.L., 1975. Multiple trait evaluation using relative's records. *J. Anim. Sci.* 43, 1188.
- HOUGH, J.D., BENYSHEK, L.L. & MABRY, J.W., 1985. Direct and correlated response to yearling weight selection in Hereford cattle using nationally evaluated sires. *J. Anim. Sci.* 61, 1335.
- POLLAK, E.J. & QUAAS, R.L., 1981. Monte Carlo study of genetic evaluations using sequentially selected records. *J. Anim. Sci.* 52, 257.
- QUAAS, R.L. & POLLAK, E.J., 1980. Mixed model methodology for farm and ranch beef cattle testing programs. *J. Anim. Sci.* 51, 1277.
- WILLHAM, R.L., 1972. Estimated Breeding Values. In: Proceedings of the Beef Improvement Federation, Eastern Regional Conf.
- WILLHAM, R.L., 1979. Evaluation and direction of beef sire evaluation programs. *J. Anim. Sci.* 49, 592.
- WILLHAM, R.L., 1982. Genetic improvement of beef cattle in the United States: Cattle, people and their interaction. *J. Anim. Sci.* 54, 659.
- WRIGHT, S., 1969. Evolution and the genetics of populations – The theory of gene frequencies. Volume II. The University of Chicago Press, Chicago and London.