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Expected early genetic gain from selection for milk yield in dairy cattle

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Summary. A matrix program to predict short term genetic gain from single trait selection for milk yield was developed. Rate of genetic gain was calculated as the annual change in the mean breeding value of all producing females. Several parameters sets representing various selection policies were used to examine situations pertinent to dairy populations of the United States. Approach to the asymptotic rates of genetic gain within the model varied with the choice of parameters, but even with consistent selection policies, predicted total genetic gain in the first 10 years was only half of the expected from classical theory. Considerable year to year variation in the rate of gain occurred. Early gains were more dependent on female selection decisions than gains during the steady state. In a two-phase model, the approach to the linear rate of gain in the second phase was accelerated by starting with an ongoing improvement program, but considerable delays still existed. Selection for sex- limited traits such as milk yield, which require pedigree selection and a waiting time for progeny test results reached asymptotic rates more slowly than previously assumed.

Key words: Genetic gain – Selection – Dairy cattle

Introduction

Use of classical theories to predict genetic progress in dairy cattle has resulted in rates which exceed estimates of actual gains. Since testing and identification of superior animals is a present cost for a future return, decisions concerning these investments depend on accurately predicting response to various selection options. Expenses for progeny testing, which improves accuracy at the expense of the delay necessary for testing, are particularly important to the dairy cattle industry.

Early attempts by Dickerson and Hazel (1944) to predict rates of progress from selection involving progeny testing alternatives emphasized the balance necessary between accuracy and the lag time associated with entry of improved genes into the population. Rendel and Robertson (1950) generalized this relationship into an expression equating the rates of gain to the sum of the selection differentials divided by the sum of the generation intervals. The sums were taken over the four paths of genetic improvement: sires to sons, sires to daughters, dams to sons, and dams to daughters.

Langholz (1973) attempted to reach a similar equation under slightly different definitions of terms. He credited genetic progress for dairy cattle only for those genes present in milking cows. Correction of an accounting error for pedigree value of young sires reduces his equations to a form which can be reconciled to Robertson and Rendel's (1950), assuming a large number of generations of selection have occurred (Dentine 1985). Implicit in these approaches were several assumptions:

(1) The variance structure of the population remained constant over time.
(2) No inbreeding depression was included in the calculations.
(3) Consistent age structures and selection policies were present during the period of interest.

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(4) Selection had been practiced long enough for a steady rate of gain to be established.

Predicted rates for dairy cattle from these models ranged from 1% to 2% annually.

Estimation of actual rates of gain from selection is complicated by environmental fluctuation. Methods to separate genetic gain were suggested by Van Vleck and Henderson (1961) and Smith (1962) under assumptions of linear genetic and environmental trends. Use of these methods resulted in rates considerably below predictions (Burnside and Legates 1967; Harville and Henderson 1967; Hintz et al. 1978; Powell and Freeman 1974; Olson and Jensen 1976). Harville and Henderson (1967) do show a possibility for a quadratic trend in their data and Lee et al. (1983) divided data into two time periods showing increasing rates in the second.

The problems inherent in attempting to optimize a selection system have been reviewed by Van Vleck (1977). Although some of these approaches examined the first three assumptions of the asymptotic theory, the concept of a steady rate of gain remained.

Searle (1961) examined the increases in gains possible through AI and extensive herd testing. He did not assume a constant rate of progress and made special note of the time period necessary to reach the upper limits of gain. From his calculations, selection would have to be practiced for over 50 years to reach within 1/2 lb/year of the maximum rate for some programs. The long delay for results from selection went unremarked at the time.

Efforts by Van Vleck (1964), Hinks (1970a, b), and Bichard et al. (1973) dealt with some of the effects of selection in the short term. Formal methods to calculate the effects of a consistent selection on genetic gain in the early years of a program and prior to reaching the maximum rate were detailed by Hill (1974) and McClintock and Cunningham (1974). The latter used a discounted expression of gene value to weight traits in an aggregate genotype on a generation basis. Hill used a matrix of breeding values which can be manipulated to represent yearly changes due to selection of parents, culling, and ageing. Both methods achieve similar results under the same assumptions (Brascamp 1978), and the predicted gains approach the asymptotic rates as the number of cycles of selection becomes large (Hill 1977).

Hill's methodology is more flexible for genetic considerations. Extensions have been added to include the effects of inbreeding by Hill (1972, 1977) and more generally by Sorensen and Kennedy (1983). Bichard (1971) and Guy and Smith (1981) used a model of a livestock dissemination system including several population tiers to calculate the lag time involved in passing genetic improvement between tiers. A similar procedure was used by Jansen et al. (1984) to trace the effects of selection for a recessive gene. Brascamp (1975, 1978) investigated returns from contrasting selection strategies for dairy populations and James (1979) suggested improvements in selection differentials possible by utilizing information on genetic subgroups already present in a selection plan.

Hill (1971) notes that "the initial response is erratic" as improvement from genes of selected individuals are distributed through the population over time but he concluded that, for a beef cattle example, good predictions can be made using the asymptotic rates rather than short term theory (1977). Since dairy cattle have both longer generation intervals and a more unbalanced reproductive rate due to artificial insemination and progeny testing, approach to the steady rate of gain should be slower than in beef cattle.

The objective of this paper was to utilize short term genetic theory to predict gains for milk yield in dairy cattle in an effort to explain the discrepancies between observed and expected rates of progress from selection.

Materials and methods

A deterministic model of the dynamics of genetic gain (Dentine 1985) was written using PROC MATRIX, a language available from Statistical Analysis Systems (SAS). Copies of the program used are available from M. R. Dentine. Procedures developed by Hill (1974, 1977) were used as a basis, but more flexibility was provided. The matrix specifying the proportion of genes coming from a given age class was not required to conform to the population age structure. Iterations representing years were separated so that a consistent selection plan over the entire time span was not necessary. The program was designed to set up a basic population with the ageing and genetic matrices as part of the infrastructure, and then to allow parameters to be varied within this population. The following assumptions were made:

(1) The selection goal was mature equivalent milk yield which was a normally distributed trait with a heritability of 0.25 and a phenotypic standard deviation of 1,000 kg.

(2) Genetic gain was defined as the annual change in the mean breeding value of the milking females. Calculations of return on investment for various alternatives would require discounting in the youngest and oldest age classes to account for the differences in actual yields.

(3) The variance structure within the population remained constant as the mean increased with selection. The variance of genetic values of young bulls was similar to the population genetic variance despite selection on pedigree values. This assumption is consistent with data given by Lee et al. (1980) on young bulls in recent use.

(4) A reasonably large population was assumed as the pool for sires and dams of young bulls. Heifer replacements and culling decisions were made within a milking herd of 100 cows. Selection differentials were estimated assuming a normal distribution of breeding values using intensities of selection based on tables provided by Becker (1975).

The probabilities of survival to second through eighth lactations, given a first lactation, were 0.73, 0.57, 0.37, 0.33, 0.17, 0.10, and 0.07. No cows were retained after an eighth lactation. The probability of a given calf being a heifer was 0.5. Heifer calves were saved from all ages of dams. Bull calves were not retained from 2-year-old dams or from matings with young bulls. Young bulls were bred to random cows to have their first offspring born when the bulls were 2 to 3 years old. After the test crop of offspring, young bulls were not used for further matings until progeny test results were known. Bulls surviving after culling based on progeny test were used for an average of 6 years to sire both sons and daughters. Culling of cows on the basis of milk production, if included, was between first and second lactations. Subsequent removal from the herd was assumed to be random with respect to genetic value for yield.

Parameters representing several selection programs were used in the matrix framework. Selections were based on estimated breeding values for mature equivalent milk yield. The initial parameter set (A) was chosen to represent a basic selection program similar to that of the present United States populations:

1) The top 2% of the cows with two or more records was used as bull dams.
2) The top 10% of the proven bulls was used as sires of young bulls.
3) The top 33% of the young bulls was retained for further service after progeny testing.
4) A random 5% of the cows was bred to young bulls.
5) There was no voluntary female culling on yield or selection of replacement calves.

A consistent selection policy for 30 years was used to investigate the behavior of the rate of genetic gain prior to reaching the asymptotic rate.

A second parameter set (B) was used to model an intensification of an ongoing program such as a shift from selection for several traits with moderate selection pressure to more emphasis on a single trait. Second phase parameters were set (A) with an increase to 10% of the cows being bred to young bulls. First phase selection over a period of 15 years included:

1) The top 20% of the cows was used as bull dams.
2) The top 50% of the proven sires was used as bull sires.
3) The top 50% of the young bulls was retained after progeny test.
4) No females were culled for production; no selection was practiced for replacements. A random 5% of the cows was bred to young bulls.

A third parameter set (C) was used to compare the results of two selection programs with the same asymptotic rates. Our purpose was to represent two options which would have been judged equivalent by classical theory. Parameter set (A) was modified to include a decrease (approximately 18% change in differentials) in young bull pedigree selection specifically designed to offset the addition of culling and heifer calf selection. Culling for production accounted for 33% of the losses of cows in first lactation. Heifer calves were retained for replacements from the top 75% of the cows. Both options included 10% of the cows bred to young bulls. The contrast would then be made for two systems of selection with slightly more male selection in one and slightly more female selection in the other.

For each parameter set, yearly and cumulative gains in milk yield were summarized and averages for the milking herd were computed. Marginal gains were calculated as average herd value in year (i) minus value in year (i−1).

Results and discussion

Modeled gains from use of parameter set (A) for 20 years are shown in Fig. 1. Predicted linear rate was 70.8 kg/year and is represented by the straight line. Expectations of the yearly genetic level approached the asymptotic rate of gain but had considerable variation in early years. Modeled genetic progress expressed as a percent of the prediction is presented in Table 1. Total gains after 10 years were only 54% of predictions. Even after 20 years of consistent selection, only 80% of the expected gains were realized.

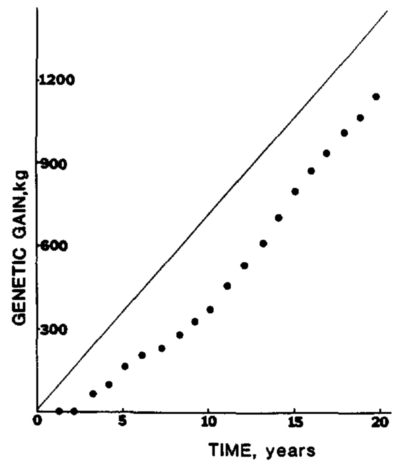

Fig. 1. Cumulative genetic gain from matrix simulation using parameter set (A)

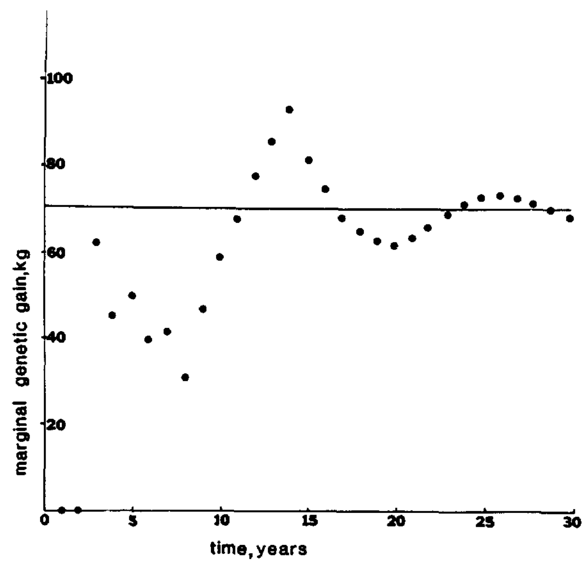

Fig. 2. Marginal genetic gains using parameter set (A)

Considerable year to year variation in rates of gain occurred as a result of the uneven flow of selected genes between the sexes. Some of the improved genes passed out of the milking population as sons and then returned when these bulls were used for service. A substantial time lag in returning genes to the females, primarily due to the time required for progeny testing, delayed the ap-

Table 1. Results of modeled selection programs: accumulated genetic gains expressed as a percent of asymptotic prediction for various selection programs

Selection scheme	Years of selection		
	10	15	20
Single trait selection (A)	54	75	80
Second phase of scheme (B)	76	86	92
Equal asymptotic schemes (C):			
More intense young sire selection	55	75	80
More intense female selection	82	92	93

proach to the uniform rate of gain when initiating an improved selection scheme.

Marginal rates of gain are graphed for a 30 year program in Fig. 2. The modeled population reacted to selection as a system in equilibrium which has been disturbed by a force (selection) and has responded with a damped harmonic approach to a new equilibrium. The amplitude of the disturbance is proportional to the amount of selection pressure applied. The lengths of the cycles are related to the generation intervals.

Marginal gains exceeded the predicted rate by as much as 23.5 kg/year. Selection decisions made in previous years were delayed in impact and finally realized in these years. These gains above expectation are not sustainable but are compensatory for early delays.

In the two-phase model, similar trends in gains were observed as under the first selection policy although the amplitude of the oscillations was reduced due to the lessened selection pressure. After 15 years, second phase policies were initiated. Even with an ongoing program already in progress, approach to the new asymptotic rate was slow. Ten years into the improved program, only 76% of the predicted progress was realized (Table 1). The model represented the intensified selection program as an instantaneous improvement. Implementing such a change as a national policy would necessarily take place over several years, which would delay the approach to the maximum rate of increase even further.

In the two schemes of selection with the same asymptotic rate (C), considerable differences were observed during the time prior to reaching the steady state. After 10 years of selection, the higher female selection plan had reached 82% of the expected gains but the higher male selection plan had realized only 55% of the predicted (Table 1). Marginal rates of gain in the time periods around year 15 were slightly larger for higher young bull selection. Even after 30 years, the differential from early gains resulted in a fairly stable 185 kg advantage for the scheme that included culling and heifer calf selection.

Previous estimates of realized genetic progress have been made under the assumption that a linear rate was the correct model. In our deterministic model, the steady rate of gain was not reached for many years. More importantly, deviations from linearity were not random nor independent, but oscillated around the expected linear rate. Use of a regression model to estimate genetic trend from the model using responses in 10 years of the second phase of (B) resulted in a best-fit slope equal to 52.7 kg which is only 75% of the asymptotic rate for this selection plan. Lee et al. (1983) noted the non-linearity of genetic trend in their data and imposed a grafted linear model which allowed for an increasing slope in later years. Estimates of actual genetic gains during their second time period (1969–1979) were 51.55 kg/year (Lee et al. 1983).

Parameter set (A) represents the initial years of a selection program for a new trait which has not been under selection previously. Since dairy cattle in the U.S. have been undergoing organized improvement programs for a long time, the model is probably not appropriate for current situations. The long delays in reaching the maximum rate of gain should be taken into consideration in cases such as efforts to improve native stock by within breed selection in countries without previous selection programs.

Use of parameter set (B) has two separate applications. Sire and cow evaluations were improved in accuracy and more widely accepted in the late 1960's and early 1970's (Specht and McGuillard 1960; Smith 1969). If the two-phase model is an approximation for this increase in the intensity of selection, the disappointing estimates for the rate of genetic gains during the early 1970's may be partly explained by the delay in approaching the asymptotic rate of gain, even in a population which has a certain amount of selection momentum.

A second possible situation modeled by the two-phase model is a change of selection goals to a correlated trait. For example, an ongoing selection program for total yield could be redirected towards protein yield in the second phase. First phase decisions might have put only moderate selection pressure on protein yield. Our model would indicate a considerable delay in reaching the maximum rate of gain for the new selection goal.

Under classical theory, selection decisions concerning female culling or replacements account for only a small portion of genetic gains in dairy cattle. In the early years of a selection program, selection of females plays a more important part, since gains from these decisions are realized quickly. Results from parameter set (C) illustrated the accumulated early genetic gains which persisted even after the steady rates were reached. Additional phenotypic gains would be realized from culling which are not included in these calculations. If positive maternal or cytoplasmic effects are important for a trait, the percent of early progress from female selection could be even higher.

Conclusions

Modeled selection response for sex-limited traits such as milk yield, which require pedigree selection and progeny testing, was dependent on historical decisions. Asymptotic rates of genetic gain were reached much more slowly than previously assumed. Considerable year to year fluctuation in expected values and rates of gain occurred as a result of uneven flow of selected genes to overlapping generations of differing length in males and females. For a two-phase model, a prior improvement program with moderate selection pressure did shorten the time required to reach the asymptote, but delays still existed which lowered the expectation of initial gains.

The proportion of gain due to separate selection decisions was not constant over time. In particular, female culling and heifer calf selection contributed more during the initial years of a selection program than predicted using asymptotic theory.

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