Estimates of Genetic Selection Differentials and Generation Intervals for Four Paths of Selection

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ABSTRACT

Estimated genetic values from an animal model based on first lactation milk records for 6000 AI Holstein sires and 1,074,971 Holstein cows born in 1981 or before were used to estimate average genetic selection differentials and generation intervals for the four paths of selection for each year of birth. Selection differentials for paths of sires of bulls, dams of bulls, sires of cows, and dams of cows averaged over all years were 405, 395, 239, and 42 kg and for the most recent 5 yr 884, 598, 235, and 28 kg. Generation intervals averaged for all years were by path 10.2, 6.4, 9.3, and 5.1 yr and for the most recent 5 yr 11.0, 6.4, 8.9, and 4.9 yr. Genetic trend based on the average selection differentials and generation intervals would be 34.9 kg/yr, but based on the latest 5-yr periods considering parents of grade cows genetic trend would be 57.2 kg/yr. Estimates of annual trend are considerably less than the potential rate of 96 kg/yr because of longer than necessary generation intervals and smaller selection differentials than theoretically possible.

(**Key words**: selection differentials, generation intervals, genetic trend)

Abbreviation key: **DB** = dams of bulls, **DC** = dams of cows, **SB** = sires of bulls, **SC** = sires of cows.

INTRODUCTION

Maximizing the rate of genetic gain is an objective of animal breeders. In dairy cattle breeding, this implies maximizing genetic gain for milk production for most producers. Rendel and Robertson (9) suggest that annual gains of up to 2% of the mean are possible. Achieving this goal requires intense and accurate selection of animals to use as parents of sires and dams while minimizing generation intervals.

Many studies have examined genetic trend by regression of estimated breeding values on time (3, 4, 7, 8) or regression of production on time (2, 6). In those studies, gain was considerably less than what is possible under ideal circumstances. Lee et al. (4) and Powell et al. (7) found a dramatic increase in rate of gain after 1968 compared with practically no genetic trend before that time.

Several studies (1, 5, 10, 11, 12) have suggested reasons for less genetic gain than expected: emphasis on traits other than milk production, particularly for fat test and classification score; nonrandom mating and treatment; low selection intensity for sires of bulls; long generation intervals for sires and dams of bulls; and high percentage of sampled sires returned to service with little selection based on production traits.

The purpose of this project was to examine the two major factors that affect actual genetic gain per year for milk production: average genetic selection differentials and generation intervals by year. These averages were determined for each of the four paths of selection (9): sires of bulls (**SB**), dams of bulls (**DB**), sires of cows (**SC**), and dams of cows (**DC**). Average yearly genetic gain was also estimated by regression of average genetic values on time.

MATERIALS AND METHODS

Data

Predicted genetic values were those calculated by Westell (13) using an animal model for 6000 bulls and 1,074,971 cows. Data included

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animals born through 1981 with lactations recorded prior to June 1983. The predicted genetic values were based on first lactation records for Holstein cows in the northeastern US. These records were for registered and grade cows with AI sires. The data for this study included solutions from the 30th (final) round of iteration for breeding values from the animal model evaluation. Solutions were considered near convergence, although Westell (13) suggested further iteration might be desirable for increased accuracy. In addition to predicted breeding values, the data contained year of birth, dam and sire identification, registry status, and animal type. The animal type information classified an animal as a bull or as a parent or nonparent cow with or without a production record.

Selection Differentials and Generation Intervals

Averages for predicted genetic values were calculated by year of birth for each selection path. Averages were calculated in two ways for SB and SC pathways: weighted by the number of progeny and unweighted. The unweighted average was considered an estimate of the average genetic value of the pool of sires available for breeding. The weighted average estimated the average of used sires, a more representative measure of a "typical" sire used to produce bulls or cows. Additionally, average predicted genetic values were computed for cows to be used as base group averages.

Selection differentials were calculated as the average difference for each of the selected groups from the average genetic value of a base by year of birth. Cows born in a given year were used as the base for comparison in calculating all selection differentials because they were an unselected group of animals. Because cows were considered unselected, they were used to estimate the average genetic value of the population for each birth year. The SB, DB, and SC paths were all compared with the corresponding average for registered cows, because all sires and their parents were registered. The base used to calculate differentials for dams varied with the type of dam, with all dams compared with all cows, grade dams compared with grade cows, and registered dams compared with registered cows.

Generation intervals were computed for each path of selection. The generation interval was defined as the age of the sire or dam of a bull or cow when the offspring was born. Average generation interval was calculated by progeny birth year, because the data set included only records available when the animal model estimates were calculated. The truncation of more recent data would lead to underestimation of intervals, because parents born more recently could have progeny only if they were born before the data set was created. Alternatively, averaging generation intervals by the offspring birth year did not bias interval estimates, because the data included all available records.

The estimated selection differentials and generation intervals were compared with differentials and intervals thought possible under optimum conditions.

Genetic Trend

Genetic trend was estimated in two ways: 1) by pooling estimates of the trend in each of the four paths of selection and 2) by analyzing the trend in the unselected population of cows. Average genetic trend for a path was calculated as the regression of average predicted genetic value for path of selection (G_{SB}, G_{DB}, G_{SC}, or G_{DC}) or cows (G_C) on time (T), where time was year of birth of the sire or dam of the bull or cow. Yearly averages of estimated genetic values were used so that each year had equal weight in estimating average selection differential, although weighted and unweighted means were used for the SB and SC paths to account for differential sire usage in each birth year. In addition, regression coefficients were computed for two time periods: all years and since 1968. Previous studies (4, 7) indicated 1968 as the approximate time when changes in genetic trend occurred. Similar trends were observed in these data.

Annual Genetic Change

Expected genetic improvement per year (Δ) was calculated using the formula suggested by Rendel and Robertson (9):

$$\Delta g = \frac{\Delta G_{SB} + \Delta G_{DB} + \Delta G_{SC} + \Delta G_{DC}}{L_{SB} + L_{DB} + L_{SC} + L_{DC}}$$

where ΔG is the estimated genetic superiority of the selected over their contemporaries in the base group born in the same year and L is the average age of the selected animals when their offspring were born.

Estimated selection differentials and generation intervals were compared with differentials thought possible under optimum conditions (Table 1). These values were chosen by the authors as realistic optimum goals.

Expected yearly genetic gain also was estimated using the regression estimates

$$\Delta g = 1/4\ (b_{G_{SB}}T + b_{G_{DB}}T + b_{G_{SC}}T + b_{G_{DC}}T), \text{ and}$$

$$\Delta g = b_{G_C}T.$$

RESULTS

Sires of Bulls

The trend for SB is clearly one of improving breeding values and selection differentials (Figure 1, Table 2). In fact, before 1964 the unweighted average breeding values for SB was smaller than that of the base group. Weighted and unweighted selection differentials for SB averaged 405 and 97 kg. However, these means include differentials for groups of sires born before 1968 that had weighted and unweighted averages of 242 and –66 kg. The selection differentials for 1967 to 1971 were considerably larger: 884 and 419 kg for weighted and unweighted averages. The weighted deviations for 1967 to 1971 are approximately what would be anticipated in an optimum case (882 kg).

The generation intervals were considerably longer than the ideal of 7 yr; the average was 10.2 yr overall and 11.0 yr for bulls born from 1974 to 1978 (Figure 2, Table 3). Breeders seem to have been using older, proven sires rather than young, newly proven sires as SB in more recent years.

The estimates of genetic trend for this path of selection, including SB born from 1955 to 1973, were 60.8 kg/yr and 53.1 kg/yr for weighted and unweighted means (Table 4). The regression estimate for SB born since 1968 was of limited value because of the few years with data after that time. The regression estimates for 1968 to 1971 were 13.3 and 29.6 kg/yr for weighted and unweighted means. Note that the coefficients of determination for the two regression estimates for the recent trend were both less than .05.

TABLE 1. Assumptions used to calculate potential selection differentials and annual genetic change.

Selection path	Accuracy	Selection intensity (%)	Genetic SD (kg)	Generation interval (yr)
Sire of bull	.75	5	570	7
Dam of bull	.65	5	570	5
Sire of cow	.85	20	570	8
Dam of cow	.65	90	570	5

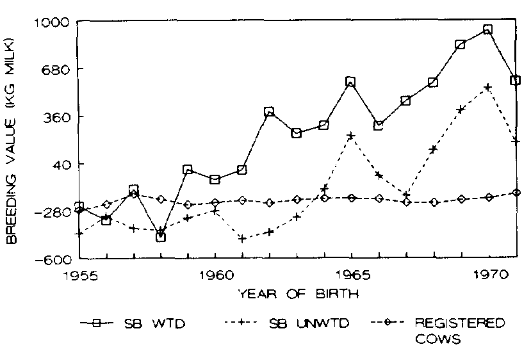

Figure 1. Average estimated breeding values of sires of bulls weighted (SB WTD) and sires of bulls unweighted (SB UNWTD) by number of sons by year of birth of sires compared with average estimated breeding values of registered cows born in the same year.

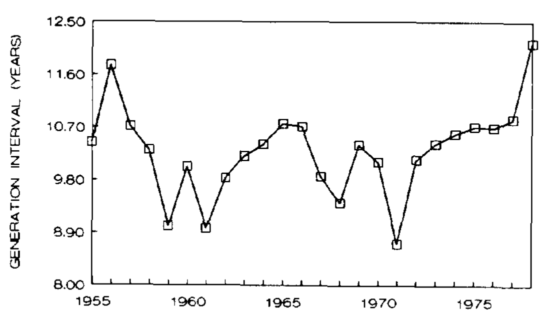

Figure 2. Average generation intervals from bulls to sires by year of birth of sires.

TABLE 2. Estimated and potential selection differentials.

Selection path	Overall average	Average for year of birth <1968	Latest 5-yr average	Potential differential
Sire of bull			(1967 to 1971)[1]	
Weighted	405	242	884	882
Unweighted	97	−66	419	
Dam of bull			(1970 to 1974)[1]	
	395	305	598	765
Sire of cow			(1974 to 1978)[1]	
Weighted				
All cows	239	123	235	678
Grade cows	288	175	250	678
Registered cows	185	66	215	678
Unweighted				
All cows	−12	−168	246	
Grade cows	−11	−172	259	
Registered cows	−19	−182	250	
Dam of cow			(1974 to 1978)[1]	
All cows	42	41	28	72
Grade cows	51	38	48	72
Registered cows	49	42	52	72

[1]Year of birth.

The overall trend estimates were much larger than those observed by Lee et al. (4) for sires born from 1960 to 1968. This may be explained by different selection programs used in the northeastern US and the availability of the Northeast sire evaluation. Recent trends observed in data were much smaller than those reported by Lee et al. (4) for sires born since 1968 (49.9 kg/yr). This may be because of the limited data available in this study since 1968.

Dams of Bulls

Average genetic selection differentials of DB compared with the registered cow base were relatively constant prior to 1968, averaging 395 kg for all years (Figure 3). Considerable improvement in selection differentials has been made since 1968; the average was 598 kg for dams born from 1970 to 1974. However, generation intervals showed little indication of becoming shorter; the average was 6.2 yr for bulls born prior to 1968 and 6.4 yr for bulls born from 1974 to 1978 (Figure 4).

The estimates of genetic trend indicated a substantial improvement in DB selection since 1968. The overall annual genetic change for DB born from 1955 to 1975 was 25.8 kg/yr, whereas the estimate of recent genetic gain (dams born from 1968 to 1974) for that path was 59.0 kg/yr (Table 4). The recent trend is substantially larger than that measured by Lee et al. (4) for DB born from 1971 to 1979, which increased by 19.3 kg/yr. Similar to the SB path, this discrepancy may be explained by different selection goals used in the Northeast and availability of the Northeast sire evaluation.

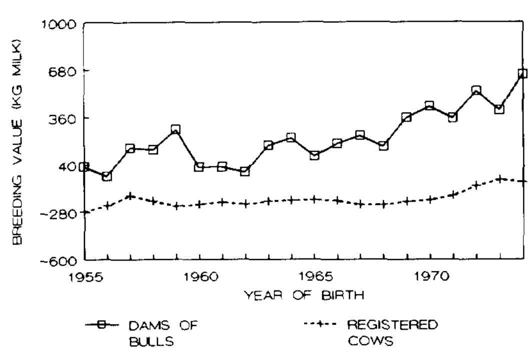

Figure 3. Average estimated breeding values of dams of bulls by year of birth of dams compared with average estimated breeding values of registered cows born in the same year.

TABLE 3. Estimated and potential generation intervals.

Selection path	Overall average	Average for year of birth <1968	Latest 5-yr average	Potential interval
Sire of bull			(1974 to 1978)[1]	
	10.2	10.1	11.0	7.0
Dam of bull			(1974 to 1978)[1]	
	6.4	6.2	6.4	5.0
Sire of cow			(1977 to 1981)[1]	
All cows	9.3	9.9	8.9	8.0
Registered cows	9.3	9.9	9.1	8.0
Grade cows	9.4	10.1	8.8	8.0
Dam of cow			(1975 to 1979)[1]	
All cows	5.1	5.2	4.9	5.0
Registered cows	5.1	5.2	5.0	5.0
Grade cows	5.0	5.1	4.9	5.0

[1]Year of birth.

Sires of Cows

The most striking feature of the SC path is the negative unweighted selection differentials for sires born prior to 1964 (Figure 5). The mean selection differentials for sires born before 1968 for weighted and unweighted averages, considering all daughters, were 123 and –168 kg.

The differentials increased dramatically in the late 1960s. The weighted and unweighted averages for sires born from 1974 to 1978 averaged 235 and 246 kg. These differentials are considerably smaller than the 678 kg thought possible. The weighted and unweighted means were nearly identical during this period, indicating that breeders had not had any opportunity to use the better sires more heavily.

The SC path was examined by grouping the registered and grade daughters separately (Figure 6). Although the fluctuations were quite similar in the registered and grade daughter groups, the weighted averages for sires of grade daughters were larger than those for registered daughters for nearly all years, 288 and 185 kg, for weighted means for grade and registered daughters.

The generation intervals from sires to cows showed very little change since an initial decrease in the late 1950s; mean intervals for all years from 1960 to 1980 were from 8.5 to 9.3 yr (Figure 7). The average sire to cow generation interval for cows born from 1977 to

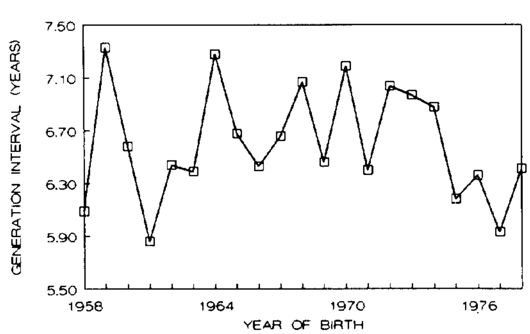

Figure 4. Average generation intervals from bulls to dams by year of birth of dams.

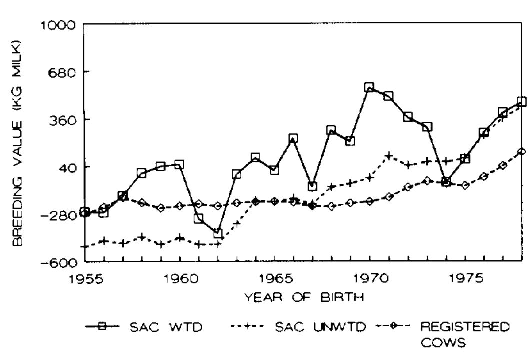

Figure 5. Average estimated breeding values for sires of all cows weighted (SAC WTD) and sires of all cows unweighted (SAS UNWTD) by number of daughters by year of birth of sires compared with average estimated breeding values of registered cows born in the same year.

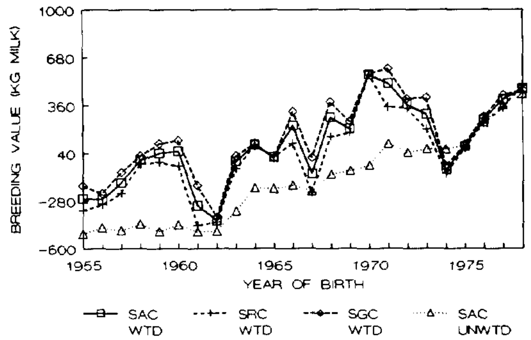

Figure 6. Average estimated breeding values of sires of all cows (SAC WTD), registered cows (SRC WTD), and grade cows (SGC WTD) weighted by number of daughters by year of birth of sires compared with average estimated breeding values of sires of all cows unweighted (SAC UNWTD) by number of daughters by year of birth of the sires.

1981 averaged 8.9 yr, somewhat closer to the optimum interval of 8 yr than the overall mean of 9.3 yr.

Estimates of genetic trend for the SC path do not show the dramatic improvement seen in the other selection paths or that suggested by earlier studies. The genetic trend using unweighted means showed both a higher rate of genetic improvement and more consistent improvement than seen using the weighted means. The estimates of trend for all years (sires born from 1955 to 1978) for SC were 27.4 and 39.5 kg/yr for weighted and unweighted means; coefficients of determination (R^2) were .51 and .93. The estimates of recent genetic trend for SC (sires born 1968 to 1978) were –4.2 and 48.2 kg/yr for weighted and unweighted means, with R^2 of .01 and .86 (Table 4), compared with 38.9 kg/yr reported by Lee et al. (4) for sires born from 1968 to 1979. The negative trend observed for the weighted path may be explained by the lack of opportunity for good proven bulls to have more daughters than those proven at the same time.

The differences between sires of registered and grade cows were small for trends in genetic improvement, although the average genetic level of sires of grade cows was greater than that of registered cows.

Dams of Cows

When the average breeding values of cows and dams are examined, the most apparent feature is the consistent improvement seen for both cows and dams as well as the superiority of dams over all cows (Figure 8). Unfortunately, the average selection differential of dams over cows is only 42 kg, again, quite low even compared with the possible differential (72 kg). This could be because of selection for traits other than milk yield and by involuntary culling levels higher than optimum. These differentials were also calculated for registered dams compared with registered cows (49 kg) and grade dams with grade cows (51 kg), and both were considerably less than the potential differential. The average differentials for 1974 to 1978 were 28, 48, and 52 kg for all, grade, and registered dams.

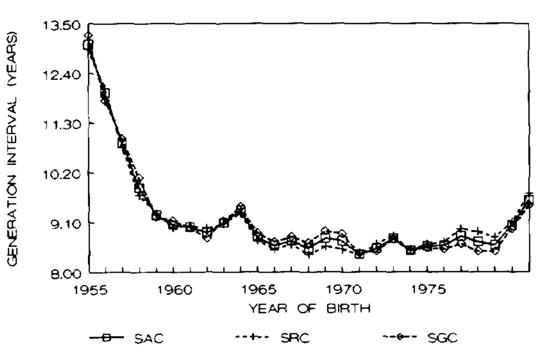

Figure 7. Average generation intervals from cows to sires for sires of all cows (SAC), registered cows (SRC), and grade cows (SGC) by year of birth of sires.

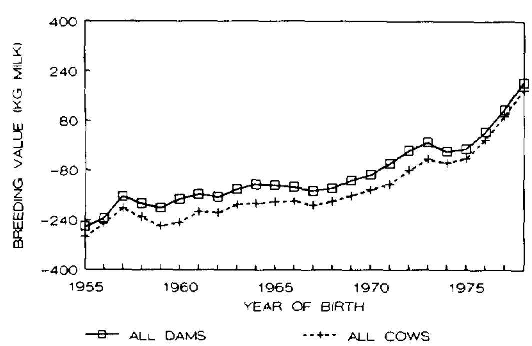

Figure 8. Average estimated breeding values of all dams by year of birth compared with average estimated breeding values of all cows born in the same year.

TABLE 4. Estimated annual genetic change for each selection path and for cows with coefficient of determination (R^2).

		Weighted		Unweighted	
Selection path	Year of birth	Estimated change	R^2	Estimated change	R^2
Sire of bull	1955 to 1973	60.8	.67	53.1	.68
	1968 to 1971	13.3	.01	29.6	.04
Dam of bull	1955 to 1975			25.8	.70
	1968 to 1974			59.0	.70
Sire of cow					
All daughters	1955 to 1978	27.4	.51	39.5	.93
	1968 to 1978	−4.2	.01	48.2	.86
Grade daughters	1955 to 1978	25.8	.47	40.4	.93
	1968 to 1978	−11.3	.04	50.0	.85
Registered daughters	1955 to 1978	28.8	.54	40.3	.93
	1968 to 1978	3.7	.01	49.2	.84
Dam of cow					
All cows	1955 to 1979			16.0	.82
	1968 to 1978			28.5	.88
Grade cows	1955 to 1979			22.0	.80
	1968 to 1978			34.0	.92
Registered cows	1955 to 1979			13.6	.82
	1968 to 1978			27.5	.86
Cows					
All cows	1955 to 1981			18.7	.83
	1968 to 1981			36.2	.95
Grade cows	1955 to 1981			21.7	.90
	1968 to 1981			35.9	.94
Registered cows	1955 to 1981			15.8	.72
	1968 to 1981			36.6	.95

The generation intervals for DC show a consistently decreasing trend; the average was 5.1 and 5.0 yr for registered and grade cows, over all years, and 5.0 and 4.9 yr for registered and grade cows born from 1974 to 1978 (Figure 9).

The estimates of genetic trend for this path showed dramatic improvement since 1968; genetic gain per year nearly doubled. For DC, the overall estimate of annual genetic change for dams born from 1955 to 1979 was 16.0 kg/yr whereas the estimate of the recent trend for dams born from 1968 to 1978 was 28.5 kg/yr (Table 4), which is very similar to results reported by Lee et al. (4), who observed a genetic trend of 25.8 kg/yr for dams born from 1969 to 1979.

Large differences in the genetic trends for dams of registered and grade cows were observed; overall estimated annual changes were 13.6 and 22.0 kg/yr for registered and grade dams born from 1955 to 1979. The annual changes for more recent years were 27.5 and 34.0 kg/yr for registered and grade dams born from 1968 to 1978.

Genetic Gain per Year

Annual genetic gain calculated using overall selection differentials and generation intervals for weighted averages and parents for all cows was 34.9 kg/yr. When we used the most recent 5-yr means with weighted averages and parents of grade cows, the expected annual genetic

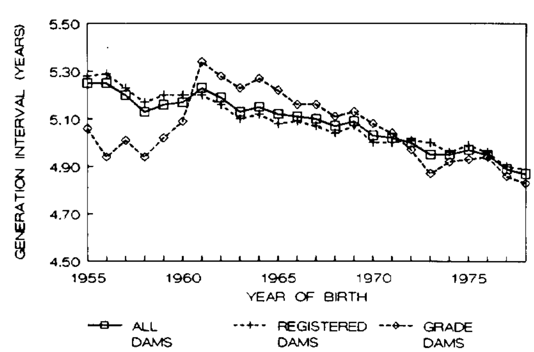

Figure 9. Average generation intervals from cows to dams for all, registered, and grade cows by year of birth of dams.

change was 57.2 kg/yr, only 60% of optimum gain.

Annual genetic improvement was estimated using trend estimated for each path of selection. Overall trend estimated (using weighted SB, weighted sires of all cows, DB, and dams of all cows as the representative paths of selection) was 32.5 kg/yr. The overall change for all cows (18.7 kg/yr) was considerably smaller, indicating that improved selection of parents may have been too recent for the selection gains to reach cows. Recent expected genetic gain was estimated using the four paths of selection as well, but overall trends for weighted means for the SB and SC paths were used instead of the recent trends because of the poor fit of the recent trends for those paths. Expected gain using recent trends for the DB and DC paths and parents of grade cows was 44.9 kg/yr, only 47% of optimum gain. Similarly, the recent estimate of genetic improvement for all cows (36.2 kg/yr) was substantially smaller than that expected from the parental trends, indicating a time lag. Improved selection in the parents is not immediately measurable in offspring.

The estimates of annual genetic change from this study agree well with those previously reported that were estimated using regression of estimated breeding values on time (3, 4, 7, 8). The overall trends in those studies ranged from 21 to 51 kg/yr estimated from trends in cows and from 36 to 98 kg/yr estimated from sire improvement.

CONCLUSIONS

Estimates of genetic change using all methods are substantially less than thought possible. The estimates from the two different methods for the selection paths yielded similar estimates. The difference between genetic trend estimates from the paths of selection and from solutions for cows indicates that, due to major improvements in genetic evaluations, estimates of genetic change may be of limited value, because the selection system is assumed to be in equilibrium. The Holstein population that was studied did not seem to be in equilibrium.

These results are limited to data through the early 1980s; the application of these data to evaluation of current selection programs must be done with caution, because these programs have almost certainly been altered since these data were recorded. The estimates of genetic improvement, genetic selection differentials, and generation intervals provide a measure of the efficiency of selection practices historically used and can help determine strengths and weaknesses in selection programs. The paths with the greatest need for improvement are those for parents of the sire: 1) generation intervals for parents of bulls appeared to be much longer than necessary, 2) these paths make up the largest portion of the total potential gain, and 3) intensity of selection appeared to be considerably less than optimum, which may be due to emphasis on traits other than milk production. Selection differentials were much smaller than thought possible for the SC path as well. Selection for traits other than milk production may be the reason in this group also. These results indicate that selection practices in that period were not optimum for maximum improvement of milk production. Decreased emphasis for nonyield traits, while reducing generation intervals, could dramatically improve genetic trend in the future.

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