The Effect of Continuous Evaluation on Genetic Response in Progeny Test Programs

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ABSTRACT

The Canadian dairy population of 1.2M cows is modelled to determine the extra genetic response from changing from standard (semi-annual) to continuous genetic evaluation. Selection for maximum estimated breeding value was truncated across mature age categories in traditional schemes and across all age categories in modern schemes. Deterministic formulas were used to predict rates of genetic response and inbreeding. Adjustments were made to account for effects of selection, inbreeding, and between age class variance on genetic variance and accuracy of selection, and for effects of correlated estimated breeding values within age classes, and finite population size on selection intensities.

If continuous evaluation is implemented in all paths, 7 to 9% higher rates of annual genetic response is predicted. Most of the expected superiority is established after one generation and continues in subsequent generations. In general, most of the advantage of CE is caused by lower generation intervals without a substantial reduction in accuracy on selected animals. By implementing CE for one year, the present value of extra profits to dairy farmers, accumulated over a 25 year planning horizon, would equal $13 to $20 for each cow in the population. The proportion of dams of AI bulls selected from first-lactation females increased from 5% to 41% with continuous evaluation. Implementation of CE in the dams of sires pathway produced the greatest improvement in genetic response.

(**Keywords:** continuous genetic evaluation, progeny testing, partial records, BLUP)

Abbreviation key:
CE = continuous genetic evaluation
DD = dams of dams
DS = dams of sires
EBV = estimated breeding value
M = modern scheme
PT = progeny test
SD = sires of dams
SE = standard genetic evaluation
SS = sires of sires
T = traditional scheme

INTRODUCTION

Progeny test (PT) programs for dairy cattle have operated effectively in many countries for decades. Genetic evaluation programs have increased in sophistication and accuracy, as methods such as contemporary comparison were replaced by sire models and eventually animal models with BLUP properties (10). Genetic progress for production traits has accelerated recently in a number of countries, leading to international

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competition between populations. Current methods of evaluation typically involve semi-annual assimilation of field data into a national database followed by execution of national BLUP animal model evaluations. Results are distributed electronically as well as by mail.

Continuous genetic evaluation (CE) is a technique currently being examined for its potential to further improve rates of genetic response through reducing delays between data collection and availability of genetic evaluations. Smith and Burnside (24) suggested that these delays could add 10 to 15% to the generation interval and decrease annual response by a similar percentage. Direct updating of bull and cow evaluations was implemented in Denmark in 1986, following a selection index approach outlined by Christensen (4). In this approach, breeding values can be updated each time new information is added. Usually, this would be done each time a herd is milk recorded. It is also possible to account for common environmental effects and heterogeneous herd variance and heritability.

With improvements in communication and computing technology, various methods have now been suggested to update animal model evaluations with new data (11, 17, 23, 29). For example, prior information on national solutions for animal genetic effects could be incorporated into mixed model equations for within herd data. The number of equations would be relatively small, and within-herd evaluations could be performed easily at milk-recording centres or perhaps even at the farm. Other methods involve continuously adding new data to national evaluations and continuing to iterate until solutions stabilize. The use of a test-day model rather than the 305-day model has also suggested possible improvement in accuracy and reduction in cost (12, 18, 19, 26). Test-day models can account for fixed effects associated directly with the day of test. These two changes may complement each other, if implemented in concert, since lactation extension factors could be eliminated and fewer tests may be needed per lactation. On its own, CE could, nevertheless, have a sizeable impact in reducing generation interval without substantially affecting average accuracy of selection.

In order to maximize benefit from CE, both implementation and application considerations must be addressed. CE could be implemented in selected pathways, such as those used in sire procurement. Alternatively, CE could be offered to some sectors of the industry that would be open to new technologies and for whom implementation would be cost-effective. To determine the optimum extent of implementation, potential improvement in the four genetic pathways must be quantified and weighed against the cost and problems associated with each. Also, CE must be readily available to the end-user in a credible and dependable format to ensure that application takes place. The purpose of this paper is to quantify the benefits of CE in terms of increased genetic response and determine which genetic pathways receive the most benefit. Effects on inbreeding rate, genetic variance, accuracy and generation interval will also be discussed. The sensitivity of the results to some of the assumptions made in this research will also be dealt with.

MATERIAL AND METHODS

The Model

There are two approaches to modelling the effect of CE on the rate of genetic response in dairy cattle. One method would involve an exact simulation of the standard evaluation (SE) process and comparing it to the CE process. In a deterministic simulation, this would involve dividing the population into very small segments and performing selection across all of them. Doing this, however, would pose problems in computing accurate selection intensities for each segment and making various adjustments to account for the effects of selection and inbreeding. Monte Carlo simulations are an alternative, but require larger computing resources and are less flexible to changes in parameters. This study followed a deterministic approach but modelled the evaluation process indirectly through the effects of SE and CE on generation interval, accuracy, genetic variance, and selection intensity. The sire evaluation process was modelled by maintaining the same accuracy, in a given age group, for SE and CE, only changing the delay between data availability and genetic evaluation. Modelling female evaluation required a different approach because breeding decisions are usually only made in the first few months of lactation. In this case, the generation interval was held constant, for a given age group, but the accuracy at the time of breeding was modified for the two evaluation methods.

The model employs deterministic formulas to simulate the Canadian breeding population of 1.2M breeding age females and 400 young sires progeny tested each year. Parameters used for selection are given in Table 1.

Table 1 Parameters for selection in traditional (T) and modern (M) progeny test schemes [1]

Parameter	Pathway [2]			
	SS	SD	DS	DD
Total number [3]	3630	3630	1,200,000	1,200,000
Traditional (T) scheme:				
Age groups available	5 to 10	5 to 10	3 to 10	1 to 10
Number available	1726	1726	396,000	876,500
Number selected [4]	33	100	800	788,850
Proportion selected	0.0197	0.0579	0.0020	0.9000
Modern (M) scheme:				
Age groups available	1 to 10	1 to 10	1 to 10	1 to 10
Number available	3210	3210	876,500	876,500
Number selected [4]	33	100	800	788,850
Proportion selected	0.0103	0.0312	0.0009	0.9000

[1] Both schemes involves progeny testing 400 young sires per year and an annual random loss of 0.05 for males and a typical age distribution of females (14). Selection is on a total merit trait with a heritability of 0.30.

[2] SS = sires of sires, SD = sires of dams, DS = dams of sires and DD = dams of dams.

[3] Total number is the number of animals in all age groups (0 to 10).

[4] The number and proportion selected were taken from Canadian and U.S. industry standards (27; Canadian Genetic Evaluation Board Release, 1992).

Details of the method are given in Lohuis et. al. (14), but will be summarized briefly here. Male and female populations were divided into eleven yearly groups, with each year group divided into two six-month age categories. A typical age distribution of females (15) and an annual random loss of 5% of sires were assumed. The oldest age group was assumed to be eleven years of age. It was assumed in this study that females were culled involuntarily for reasons including reproduction, health, and other management problems. Selection was on a total merit index with a base population heritability of 0.30. Truncation selection on estimated breeding value (EBV) (EBV = 2 x estimated transmitting ability) was practised in four pathways of selection: sires of sires (SS), sires of dams (SD), dams of sires (DS) and dams of dams (DD). Differences in genetic means (μ) between age categories were derived from the rate of genetic response occurring in the previous generation. Optimised selection across all available age categories was performed using the algorithm outlined by Ducrocq and

Quaas (7), in which genetic merit of parents is maximised by truncation selection of the highest EBV from all age categories. After selection, rate of genetic response and genetic variances in the male and female populations were re-calculated and used in the next iteration of the model. Each iteration approximated one generation of selection.

To arrive at a starting point for alternative schemes, a traditional PT with SE was assumed for the population. Without adjustments for inbreeding, this population remained under constant selection until asymptotes were approached for sire variance, dam variance and annual genetic response. The convergence criterion was 1×10^{-4} genetic s.d. units. Convergence was reached in under 10 cycles of selection.

Both traditional (T) and modern (M) PT schemes, are used for comparisons between SE and CE. The T scheme involves selection of only milking females as bull dams and males with a progeny test as sires of cows and sires of sons. The M scheme considers all post-pubertal age categories for selection for both sires and dams. In both schemes, it was assumed that one-quarter of the female population were bred to unproven young sires for progeny testing purposes. SE was defined as a national BLUP animal model evaluation done on a semi-annual basis, whereas CE involves continuous updating of a national database and continuous (or very frequent) computing of BLUP animal model solutions. The model used to approximate SE and CE, in fact, models the effect of the two evaluation systems on generation interval, accuracy, selection intensity, and genetic variance. The assumptions used are given in Table 2.

Table 2 A description of standard (SE) and continuous evaluations (CE) [1]

	Standard	Continuous
Information for males: [2]		
complete records only	A and B	A and B
complete and/or part records [3]	C, D, E	C, D, E
delay [4]	5 months	2 weeks
Information for females: [2]		
complete records only	A, B and F	A and B
complete and/or part records [3]	C and D	C, D and F
delay [4]	5 months	2 weeks

[1] Standard evaluation refers to national BLUP animal model evaluations conducted every 6 months. Continuous evaluations are standard evaluations continuously updated.

[2] Information sources:
A - Maternal grandsire: 200 daughters, 2 to 3 records
B - Maternal granddam: 2 to 3 records
C - Sire: 50 to 200 daughters, 1 to 3 records
D - Dam: 1 to 3 records
E - 50 to 200 Daughters: 1 to 3 records
F - Self: 1 to 8 records

[3] Part records were made up of information from the first 2 months of lactation.

[4] The delay was the average interval between data collection and dissemination of evaluations.

In semi-annual evaluations, the delay between data collection and the next evaluation varies from 0 to 6 months with a mean delay of 3 months, with the assumption that cows are not bred on a seasonal basis. It was assumed that data assimilation and computing required 1.5 months and dissemination of evaluations required 2 weeks. Therefore, the average delay between collection of data and availability of evaluations was assumed to be 5 months for SE and 2 weeks for CE (one week for computing and one week for dissemination.) The resulting difference in evaluation delay between SE and CE was 4.5 months. To test the sensitivity of these assumptions, the 1.5 month delay required for computing of SE was removed reducing the difference between evaluations to 3.0 months.

Both T and M schemes were applied in practical and efficient modes. The efficient mode assumed females first calved at 24 months and maintained a 12 month calving interval thereafter, while the first crop of daughters from PT sires calved 48 months after birth of the sire. In practical mode, six months were added to the age of parents, in each age group, at the time of selection. It was assumed that selection decisions are made with results from the most recent evaluation in mind. Scenarios involving increased SE frequency (e.g. quarterly evaluations) were not considered in this study, but it was assumed that such procedures would result in intermediate increases in rate of genetic response. Many American AI companies already perform internal evaluations 3 months after national evaluation runs.

Accuracy of Evaluation

Accuracy (r) of evaluation for each 6 month age category was calculated for males and females using selection index techniques to approximate those in an animal model. The assumptions and details are in the Appendix. Since extended (partial) records are presently used in SE, the same information was used to calculate sire accuracies for CE, only the evaluation delay was shortened by 4.5 months (Table 2). For the female population, it was assumed that breeding decisions were made after 2.5 months of lactation. With CE, this partial record would be included in the evaluation, but in SE (under current Canadian milk recording rules) it would not. All other information sources remained the same and the difference in evaluation delay was the same as for sires. Partial records, at 60 days in milk, were assumed to have a phenotypic and genetic correlation with complete records of 0.78 and 0.83, respectively (1), although Wilmink (28) and VanRaden et al. (25), using more precise lactation prediction methods, have reported higher correlations between 305-day yields projected or expanded from partial records and realized 305-day yields. Genetic correlations between first test day records and complete lactation records of 0.87, 0.77, and 0.84 were also reported by Pander et al. (18) for milk, fat and protein yield. It was assumed that 305 days in milk constituted a complete lactation. The variance of partial records was taken as 73% of completed records (1). Both partial and complete records were assumed to have a heritability of 0.30 and a repeatability of 0.60. From these assumptions, the phenotypic correlation can be derived (Appendix) between a complete record and a part record from a different lactation, and, in this case, had a value of 0.44. To test the sensitivity of these assumptions, the heritability of partial records were reduced by one-third (to 0.20) to determine the effect on results. As well, genetic correlations between partial and complete records were also reduced by one-third (to 0.55).

Since the population has undergone selection with animals ranked by a BLUP animal model, r was adjusted for loss of variance due to selection following Dekkers (6) as:

$$r^{*} = \sqrt{1 - (1 - r^{2})\sigma_0^{2} / \sigma^{*2}} \qquad [1]$$

where σ_0^2 is the genetic variance in the unselected population and σ^{*2} is the present genetic variance. Standard deviations of EBV (σ^{*}_{EBV}) were then calculated as $r^{*}\sigma^{*}$ for each age category.

Genetic Response

Selection intensity was adjusted for finite population size according to the approximation by Burrows (3) and for correlated EBV among relatives within cohorts according to the approximation by Rawlings (20) revised by Meuwissen (16). Variance was adjusted for the effects of selection, inbreeding, and differences in selected means from different age categories (14). The inbreeding coefficient in the starting population was taken as 0.034 for the North-American Holstein population (30). Loss of variance due to inbreeding was accounted for, but no adjustments were made for inbreeding depression.

Genetic response per generation, after all adjustments, was calculated across all pathways according to standard procedures (21).

$$R^* = \sum_{j=1}^{4} .25 \left[\sum_{i=1}^{m} (w_{ij} I^*_{ij} r^*_{ij}) \right] \sigma^*_j \qquad [2]$$

where m is the number of age categories, and w_{ij} is the proportion of selected animals originating from the ith age category in the jth pathway. I^*_j is the selection intensity, adjusted for correlated breeding values and finite population size, and r^*_j and σ^*_j are the accuracy and genetic standard deviation, in path j, adjusted for selection and inbreeding. The rate and coefficient of inbreeding was calculated from the effective number of sires and dams following Falconer (8). The effective number of parents was approximated from the number of parents selected and the average selection intensity and intra-class correlation between EBV (22). For the SS and SD pathways, $\sigma^*_j = \sigma^*_S$, and for the DS and DD pathways, $\sigma^*_j = \sigma^*_D$. In the SD pathway, I^*_j was adjusted for the proportion of females sired by untested young sires (P_{YS}), for which selection intensity is zero, as $I^*_j(1 - P_{YS})$.

Annual genetic response was then calculated as:

$$\Delta G = R^* / \left[\sum_{j=1}^{4} .25 \left(\sum_{i=1}^{m} w_{ij} L_{ij} \right) \right] \qquad [3]$$

where L_{ij} is the generation interval of the ith age category in the jth pathway.

Annual genetic responses were calculated for T and M schemes with SE and with CE. Both practical and efficient modes of selection were considered. Since national breeding strategy normally involves a longer planning horizon than corporate strategy, annual genetic responses were calculated over 5 cycles of selection (approximately 5 generations) starting from a T scheme with SE. To determine which pathways were affected most by CE, each pathway was changed from SE to CE independently and in combination with one other pathway.

RESULTS

Accuracy of Age Categories

The resulting unadjusted accuracies for males and females, in efficient selection mode, with SE and CE are shown in Figure 1. In the female population, the largest difference between CE and SE occurs at 2.2 years of age when partial lactation records become available with CE, and unadjusted accuracy is 13% higher than

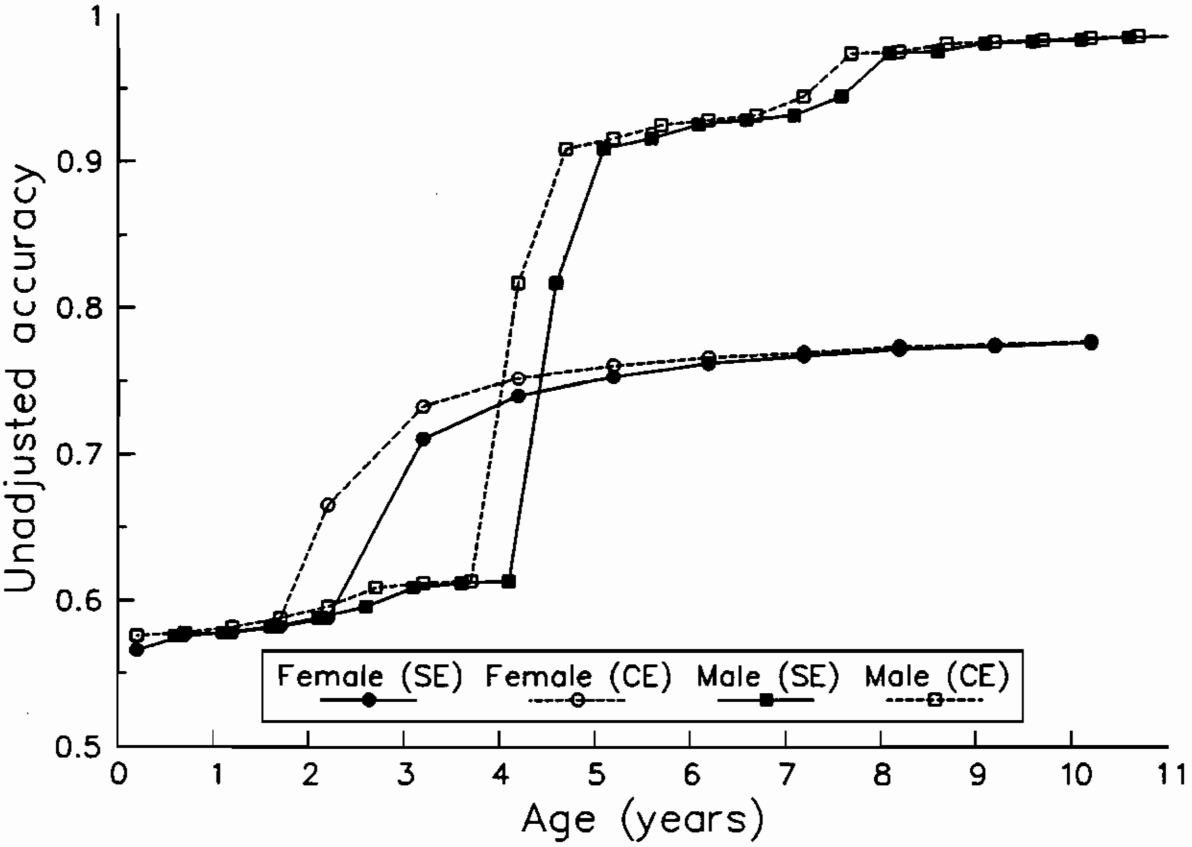

Figure 1 Accuracies (unadjusted for selection) for males (closed squares) and females (closed circles) with standard evaluation (SE), or for males (open squares) and females (open circles) with continuous evaluation (CE)

with SE. Accuracies adjusted for the effects of selection are 22% higher with CE. This difference diminishes quickly in subsequent lactations when complete lactation information becomes available. In the male population, the only difference is the delay between data collection and dissemination of evaluations. Therefore, the difference appears in Figure 1 as a 4.5 month shift. The largest difference in accuracy (33% higher) occurs at 4.2 years of age when partial records become available from the daughters with CE. Accuracies, adjusted for the effects of selection, are up to 74% higher for CE at this age. This difference disappears within one year, but a small difference of 3% (5% when adjusted for selection) reappears between years 7 and 8 when the second crop of daughters begin milking. However, since younger age groups were selected under CE, the net effect on accuracy was very small. The average adjusted accuracy of all animals selected as parents changed by less than a factor of 0.02 and, in most cases, it increased. Because the effect on average accuracy was negligible, the error of prediction associated with SE and CE differs very little. Therefore, the most advantageous scheme will be the one that shows the highest genetic response as estimated from deterministic simulation (hereafter referred to as genetic response.) It should be noted that although genetic response estimated by deterministic simulations quite often overestimates the actual genetic response, the comparison between schemes is likely more accurate and of greater importance.

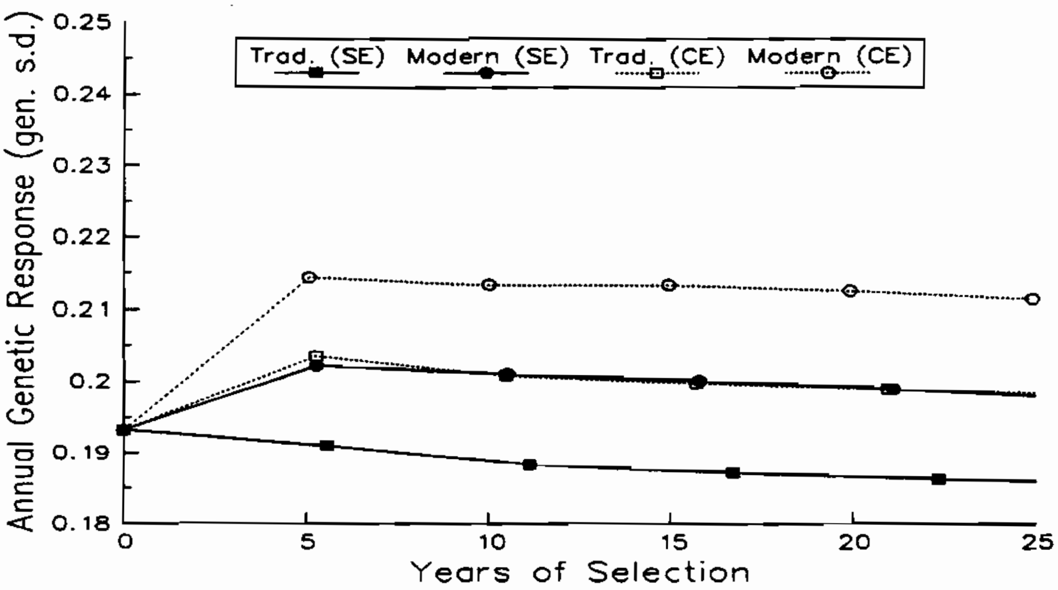

Figure 2 Annual genetic response for traditional (T) and modern (M) schemes with continuous (CE) and standard (SE) evaluations in practical mode

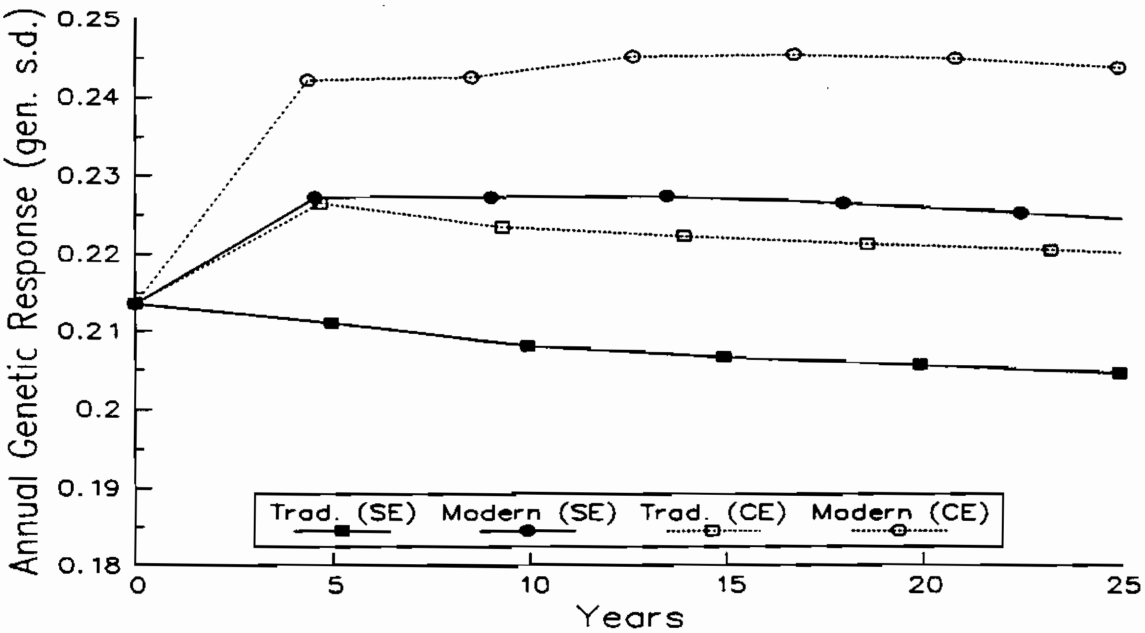

Figure 3 Annual genetic response for traditional (T) and modern (M) schemes with continuous (CE) and standard (SE) evaluations in efficient mode

Genetic Response

The effects of CE on annual genetic response for T and M schemes can be seen in Figure 2, for practical mode, and in Figure 3 for efficient mode. Since the different schemes vary in regards to generation length, the annual genetic response is plotted against years of selection rather than cycles (generations) of selection. The starting values for all schemes were those from the T scheme, with SE, at equilibrium. Equilibrium was reached in under 10 cycles of selection for both practical and efficient modes. Due to the loss of variance from inbreeding, the T scheme with SE gradually declines, but with CE there is an initial increase in annual response of 6.6 and 7.3% followed by a gradual decline. Most of the advantage over SE is established in the first generation but the relative advantage continues in subsequent generations. When a M scheme begins with SE, the initial advantage is similar to that observed from the T scheme with CE. In practical mode, this relationship holds in subsequent generations, but in efficient mode (Figure 3), the advantage of scheme M increases. The reason is that when the annual response is high enough, in a modern scheme, the relative advantage and contribution of younger age categories increases. When greater numbers of parents come from younger age categories, the selection intensity rises and the between-group variance increases and adds to the genetic variance. In efficient mode, this additional variance more than compensates for the variance lost due to inbreeding and selection. However, the inbreeding level will eventually increase to the point where variance and annual response start to decrease (generation 6). The largest annual response is achieved from the M scheme using CE.

The relative advantage after 5 generations, for practical schemes, can be found in Table 3. CE results in 6.8 and 7.0% larger annual response for T and M schemes, respectively, with similar increases in rate of inbreeding. Average generation interval decreased by 6.4 and 6.8%, while genetic variances, for both sires and dams, were hardly affected. In the sire pathways, average accuracy (weighted across age categories) decreased but less than the decrease in generation interval. In the DS pathway, generation interval decreased 8 to 13% with little change in accuracy. In the DD pathway, accuracy was increased 9 to 10% with no effect on generation interval. In general, most of the advantage of CE is caused by lower generation intervals without a substantial reduction in accuracy. In all but the SS pathway, juvenile categories contributed more when CE was in effect. The largest change in selection was in the DS pathway. Females between 2 and 3 years of age produced 5% of bulls for AI with SE, but this increased to 41 and 40% with CE, for T and M schemes, respectively. This was mostly due to the availability of evaluations based on partial records before the female was re-bred.

When these schemes were considered in efficient mode (Table 4), CE lead to slightly greater increases in genetic response (7.8 and 8.8%) for T and M schemes. However, the rate of inbreeding increased faster than genetic response when CE was implemented. In this type of scheme, inbreeding rates were quite low so this would likely not pose a problem. Selection of parents from various age categories followed the same pattern found in practical mode, but a greater proportion of juveniles were selected. In the M scheme, the proportion of juvenile bulls used as SS climbed to almost 7% and the proportion used as SD (outside of progeny testing) reached over 45% for CE.

Rates of genetic response and inbreeding relative to the T scheme with SE are given for all schemes in Table 5, after 1 and 5 generations. The table illustrates that by changing to CE and the M scheme simultaneously, annual response increased 14 and 20% by generation 5 for practical and efficient modes, respectively. In the efficient mode, however, inbreeding rate increased by 24%. When in efficient mode, the rate of inbreeding was increased more by a change to an M scheme than a change to CE.

Table 3 Annual genetic response (ΔG), after 5 generations, generation interval (L), annual inbreeding rate (ΔF), and genetic variance of sires and dams for practical schemes [1]

	Traditional PT		Modern PT	
	Standard	Continuous [2]	Standard	Continuous [2]
ΔG [3]	0.186	(1.068)	0.198	(1.070)
L_{AVG}	5.605	(0.936)	5.343	(0.932)
ΔF x 1000	0.762	(1.070)	0.802	(1.072)
σ_S^2 [3]	0.661	(1.005)	0.670	(1.000)
σ_D^2 [3]	0.764	(1.002)	0.783	(1.010)
SS pathway:				
r_{TI}	0.857	(0.997)	0.857	(0.992)
L	7.253	(0.941)	7.206	(0.928)
W_{4+}	1.000	1.000	1.000	1.000
SD pathway: [4]				
r_{TI}	0.862	(0.995)	0.778	(0.929)
L	6.035	(0.938)	5.574	(0.894)
W_{4+}	1.000	1.000	0.882	0.810
DS pathway:				
r_{TI}	0.603	(0.981)	0.572	(1.030)
L	4.979	(0.871)	4.445	(0.923)
W_1	-	-	0.195	0.095
W_2	0.051	0.413	0.049	0.398
W_3	0.577	0.401	0.477	0.358
W_{4+}	0.372	0.187	0.280	0.150
DD pathway:				
r_{TI}	0.450	(1.100)	0.457	(1.090)
L	4.151	(1.000)	4.147	(1.001)

[1] Adjusted accuracy (r_{TI}), generation interval (L), and age category contributions (W_i) are given for each genetic pathway: SS=sires of sires, SD=sires of dams, DS=dams of sires, DD=dams of dams. Contributions to the DD path were not affected and not shown.

[2] Values in brackets are expressed as a proportion of those for standard evaluations.

[3] Annual genetic response and genetic variances for sires (σ_S^2) and dams (σ_D^2) are given in base population genetic s.d. units.

[4] The SD pathway values do not include 25% young sire usage.

Table 4 Annual genetic response (ΔG), after 5 generations, generation interval (L), annual inbreeding rate (ΔF), and genetic variance of sires and dams for efficient schemes [1]

	Traditional PT		Modern PT	
	Standard	Continuous [2]	Standard	Continuous [2]
ΔG [3]	0.205	(1.078)	0.225	(1.088)
L_{AVG}	5.024	(0.925)	4.495	(0.910)
ΔF x 1000	0.850	(1.081)	0.953	(1.105)
σ_S^2 [3]	0.663	(1.006)	0.679	(1.007)
σ_D^2 [3]	0.768	(1.004)	0.811	(1.018)
SS pathway:				
r_{TI}	0.853	(0.993)	0.850	(0.945)
L	6.670	(0.922)	6.516	(0.891)
W_{4+}	1.000	1.000	1.000	0.933
SD pathway: [4]				
r_{TI}	0.856	(0.996)	0.629	(0.887)
L	5.416	(0.937)	4.238	(0.839)
W_{4+}	1.000	1.000	0.661	0.548
DS pathway:				
r_{TI}	0.599	(0.984)	0.562	(1.054)
L	4.373	(0.852)	3.591	(0.940)
W_1	-	-	0.293	0.155
W_2	0.074	0.465	0.086	0.441
W_3	0.597	0.385	0.420	0.302
W_{4+}	0.329	0.151	0.201	0.102
DD pathway:				
r_{TI}	0.453	(1.101)	0.456	(1.083)
L	3.638	(1.000)	3.634	(1.000)

[1] Adjusted accuracy (r_{TI}), generation interval (L), and age category contributions (W_i) are given for each genetic pathway: SS=sires of sires, SD=sires of dams, DS=dams of sires, DD=dams of dams. Contributions to the DD path were not affected and not shown.

[2] Values in brackets are expressed as a proportion of those for standard evaluations.

[3] Annual genetic response and genetic variance of sires (σ_S^2) and dams (σ_D^2) are given in base population genetic s.d. units.

[4] The SD pathway values do not include 25% young sire usage.

Table 5 Annual genetic response and inbreeding rate (in brackets) relative to a traditional PT scheme with standard evaluations[1] after 1 and 5 generations

	Generation 1		Generation 5	
	Standard	Continuous	Standard	Continuous
Practical mode:				
Traditional PT	1.000 (1.000)	1.066 (1.057)	1.000 (1.000)	1.068 (1.070)
Modern PT	1.059 (1.057)	1.123 (1.102)	1.065 (1.052)	1.140 (1.129)
Efficient mode:				
Traditional PT	1.000 (1.000)	1.073 (1.064)	1.000 (1.000)	1.078 (1.081)
Modern PT	1.076 (1.095)	1.147 (1.142)	1.101 (1.121)	1.198 (1.239)

[1] Standard evaluations refer to national BLUP animal model evaluations conducted every 6 months. Continuous evaluations are standard evaluations continuously updated.

Table 6 Annual genetic responses for standard evaluation[1] and continuous evaluation for selected pathways after 5 generations of selection for traditional (T) and modern (M) progeny test schemes

	Standard Evaluation	Continuous evaluation in pathways [2]					
		SS	SD	DS	DD	SS + DS	All
Practical mode:							
T scheme	0.186	(1.017)	(1.013)	(1.035)	(1.001)	(1.054)	(1.068)
M scheme	0.198	(1.022)	(1.017)	(1.028)	(1.000)	(1.053)	(1.070)
Efficient mode:							
T scheme	0.205	(1.022)	(1.016)	(1.040)	(1.001)	(1.062)	(1.078)
M scheme	0.225	(1.035)	(1.027)	(1.026)	(1.000)	(1.054)	(1.088)

[1] Annual genetic responses are expressed in base population genetic s.d. units.

[2] Results for continuous evaluations (in brackets) are expressed as a proportion of values for standard evaluation.

Effect on Pathways

The effect of limiting CE to selected pathways or combinations of pathways is illustrated in Table 6. The largest improvement in annual response (4%) from CE was achieved in the DS pathway. There was a greater improvement when the T scheme was operating, because many juvenile females were already selected in M schemes. The SS pathway showed slightly more improvement from CE than the SD path. Little change resulted from changing the DD pathway to CE. However, when scheme M was in place, the relative improvement resulting from continuously evaluating sires increased. This is likely due to lower generation intervals which magnified the impact of reducing the evaluation lag by 4.5 months. If CE were available only to AI personnel for the selection of parents of bulls (SS + DS), the majority (61 to 79%) of the improvement from CE would be realized. Since the impact of these pathways is already large, this is not surprising. Very little improvement would be realized in the DD path because the selection pressure is relatively low compared to the other paths.

Sensitivity of Assumptions

In modern PT schemes, when the assumption regarding the delay between data collection and availability of SE was reduced from 4.5 to 3.0 months, the extra annual genetic response from changing to CE was reduced to 5.6 and 7.2% for practical and efficient modes, respectively. This was approximately 20% lower than the predicted extra response when normal assumptions were used (Table 7). Genetic response was moderately sensitive to this change because, even with a 3 month delay with SE, partial records were not incorporated into female evaluations. When the assumption regarding h^2 for part records was reduced from 0.30 to 0.20, the extra response from changing to CE was reduced to 5.7 and 6.7% for practical and efficient modes, respectively. When the assumption regarding the genetic correlation between partial and complete records was reduced from 0.83 to 0.55, the extra response from CE was reduced to 5.2 and 6.6%. Although h^2 and genetic correlations were reduced by 33%, the largest decrease in extra response was by 24 and 26%, respectively, because both SE and CE responses were affected. Of course, if assumptions were altered in the opposite direction, larger increases in genetic response would be expected from changing to CE.

Table 7 Sensitivity of annual genetic responses, when assumptions change, and responses relative to standard evaluations (in brackets) for modern PT schemes after 5 generations [1]

	Practical Mode		Efficient Mode	
Assumptions [2]	Standard	Continuous	Standard	Continuous
Normal assumptions	0.198 (1.000)	0.211 (1.070)	0.225 (1.000)	0.245 (1.088)
Difference in delay equals 3 months	0.200 (1.000)	0.211 (1.056)	0.229 (1.000)	0.245 (1.072)
$h^2_{part} = 0.20$	0.196 (1.000)	0.207 (1.057)	0.223 (1.000)	0.238 (1.067)
$r_G = 0.55$	0.192 (1.000)	0.202 (1.052)	0.218 (1.000)	0.2324 (1.066)

[1] Standard evaluations refer to national BLUP animal model evaluations conducted every 6 months. Continuous evaluations are standard evaluations continuously updated.

[2] The normal assumptions are those stated in the text. The other 3 scenarios test the sensitivity of the results to assumptions about evaluation delay, heritability (h^2) of partial records, and genetic correlation (r_G) between part and whole records.

DISCUSSION

In replacing SE with CE, estimated annual genetic response increased by 6.8 to 8.8% (0.013 and 0.020 genetic s.d.). In concert with optimized selection across all age categories, response was improved by up to 19.8% (0.041 genetic s.d.). It should be mentioned that if SE is improved by simply increasing the frequency of evaluations or reducing the delay between data collection and evaluation, extra response would result as well. In Canada, the expansion of partial records with less than 90 days in milk (25) would also boost the genetic response from SE. However, these improvements would not likely benefit evaluation of females because, in most cases, evaluations would still not be available when breeding decisions need to be made.

To determine the value of CE to dairy farmers, a one standard deviation of index estimated transmitting ability (sires with 50 effective daughters) was assumed to be worth $59.94 extra profit per lactating daughter, based on the present Canadian pricing scheme, in which milk price is approximately $ 0.50 (Cdn.)/L (9; Gibson, personal communication). The profit was based solely on the production components and no value was placed on type. With an accuracy of 0.907 for sires with 50 effective daughters, the value of one genetic standard deviation in the female population would, therefore, be worth ($59.94 x 2) ÷ 0.907 = $132.17. Therefore, for each year of genetic response, the annual increase in genetic response for profit from CE would be $1.72 to $2.64. Over the entire dairy industry, this benefit would be considerable. Assuming that monetary value of extra genetic improvement ($ΔG) only disseminates into the population 9 years later and that a time horizon of 25 years is taken, the present value future benefits (PVFB) of applying CE for one year can be approximated following Brascamp (2):

$$PVFB = \$\Delta G \sum_{t=9}^{25} \left(\frac{1}{1+r}\right)^{t} \qquad [4]$$

where r is the discount rate (5% is assumed) and t is the year the benefit is received. In this case, using CE for one year results in a PVFB of $13.13 to $20.15 per cow. Over the Canadian dairy population of 1.2M cows this benefit would be worth $16M to $24M (Canadian). If the benefit is disseminated into the population sooner, PVFB will be greater. Considering that the annual extra cost of computing resources and staff required to carry out CE would certainly be less than $0.5M, implementing CE, at least in the SS and DS pathways, would be a sound investment. Implementing CE in the SD and DD pathways would be more costly and difficult to accomplish, because the way semen is marketed and delivered would need to be changed.

It has been shown that relatively small genetic differences between competing A.I. organizations could increase their economic returns from semen sales disproportionately (5). In the context of breeding programs competing for an international market of semen, embryos, and livestock, the advantage could be large. The benefits quantified above may be overestimated in situations where notable quantities of semen are imported from countries without CE, or where AI companies already do more frequent internal evaluations on all males and females. The benefit of CE would also be reduced if dairy farmers refuse to buy semen on a more frequent basis or are unwilling to use semen from bulls proven on the basis of partial records. However, the estimates may also underestimate the true value of CE since conservative estimates of the correlation between whole and partial records were used, and the simulation divided the lifespan of males and females into 6 month segments. In reality, CE would provide a smoother change in accuracy and likely greater differences between CE and SE. The estimates above apply primarily to production traits because the data is collected throughout a cow's lifetime. With conformation, reproduction or health traits, data is collected less frequently and the extra genetic response from CE would be less.

CE is equally important for males and females except when modern schemes are operating. The most benefit would be realized by implementation of CE in selection of sires and dams of AI bulls. However, significant benefits to dairymen may be lost if steps are not taken to implement CE in the SD path. As well, a two-tier evaluation system may not be considered equitable by cattle breeders. Certainly, implementing CE in the sires of dams path would transform the process of marketing semen. The semi-annual production of present day sire catalogues could be replaced by 'electronic catalogues' for males and females. The marketing and bull purchasing 'bottlenecks' at certain times of the year could be eliminated, thereby increasing efficiency. To assure easy use of CE and avoid confusion, widespread accessability of computers and appropriate software will be necessary for farmers, AI personnel and foreign buyers. One suggested method of incorporating CE into everyday farm use is to provide computer software to farmers as part of the service from milk recording organizations. This software could automatically access the results of CE from a computer bulletin board. For example, computer mating packages could make use of the latest CE results each time a breeding decision is made. The potential of integrating electronic daily milk recording information into a CE network should also be considered as a way of boosting accuracy and reducing costs.

On its own, CE would have a sizeable impact in reducing generation interval without significantly reducing average accuracy of selection. Other breeding strategies, such as the formation of centralized MOET nucleus herds, also reduce generation intervals through maximizing the impact of juvenile age categories. However, schemes that rely heavily on juvenile age categories become limited by inbreeding rather than reproductive performance when nucleus size is small (13). By incorporating CE into genetic evaluation procedures, information from the performance of individuals is used more efficiently with acceptable increases in rates of inbreeding.

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APPENDIX

The phenotype of a partial record at 60 days in milk (P_{pa}) and a complete record (P_{comp}) were defined as separate but correlated traits, as follows:

$$P_{pa} = G_{pa} + PE_{pa} + TE_{pa}$$

$$P_{comp} = G_{pa} + G_{re} + PE_{pa} + PE_{re} + TE_{pa} + TE_{re}$$

where G, PE and TE are genetic, permanent and temporary environmental effects, respectively, and re refers to the remaining part of the lactation. Assuming no genotype by environment interactions, the variance (V) - covariance (COV) structure between part and complete records from lactation a is as follows:

$$\begin{array}{c|cccccc|}
 & G^a_{pa} & G^a_{re} & PE^a_{pa} & PE^a_{re} & TE^a_{pa} & TE^a_{re} \\
G^a_{pa} & V(G^a_{pa}) & COV(G^a_{pa},G^a_{re}) & 0 & 0 & 0 & 0 \\
PE^a_{pa} & 0 & 0 & V(PE^a_{pa}) & COV(PE^a_{pa},PE^a_{re}) & 0 & 0 \\
TE^a_{pa} & 0 & 0 & 0 & 0 & V(TE^a_{pa}) & 0
\end{array}$$

Assuming G and PE effects on part records remain constant throughout the life of a cow (i.e. part records in different lactations are considered to be the same trait), then the variance (covariance) structure between a complete record from lactation *a* and a part record from lactation *b* is as follows:

$$\begin{array}{c|cccccc|}
 & G^a_{pa} & G^a_{re} & PE^a_{pa} & PE^a_{re} & TE^a_{pa} & TE^a_{re} \\
G^b_{pa} & V(G^a_{pa}) & COV(G^a_{pa},G^a_{re}) & 0 & 0 & 0 & 0 \\
PE^b_{pa} & 0 & 0 & V(PE^a_{pa}) & COV(PE^a_{pa},PE^a_{re}) & 0 & 0 \\
TE^b_{pa} & 0 & 0 & 0 & 0 & 0 & 0
\end{array}$$

Then the phenotypic correlation between a complete record from lactation *a* and a part record from lactation *b* is as follows:

$$r_{(P^a_{comp},P^b_{pa})} = r_{(P^a_{comp},P^a_{pa})} - (1 - R_{pa})\sqrt{V(P_{pa})\ /\ V(P_{comp})}$$

where r is the correlation and R_{pa} is the repeatability of partial records, at 60 days in milk.

It was assumed that $R_{comp} = R_{pa} = 0.60$ and heritability (h^2) was assumed to be 0.30 for both traits. If the correlation between P_{comp} and P_{pa} of the same lactation is 0.78 and the ratio $V(P_{pa})$ / $V(P_{comp})$ is 0.73 (1), then the phenotypic correlation between part and complete records from different lactations is equal to 0.44. Standard selection index procedures for multiple traits were then employed to calculate accuracies of selection. To test the sensitivity of these assumptions, h^2 was reduced to 0.2, and the correlation between G_{comp} and G_{pa} was also reduced to 0.55.