Genetic Improvement of Total Milk Yield and Total Lactation Persistency of the First Three Lactations in Dairy Cattle

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ABSTRACT

The objective of this study was to compare 6 selection criteria in terms of 3-parity total milk yield and 9 selection criteria in terms of total net merit (H) comprising 3-parity total milk yield and total lactation persistency. The 6 selection criteria compared were as follows: first-parity milk estimated breeding value (EBV; M1), first 2-parity milk EBV (M2), first 3-parity milk EBV (M3), first-parity eigen index (EI₁), first 2-parity eigen index (EI₂), and first 3-parity eigen index (EI₃). The 9 selection criteria compared in terms of H were M1, M2, M3, EI₁, EI₂, EI₃, and first-parity, first 2-parity, and first 3-parity selection indices (I₁, I₂, and I₃, respectively). In terms of total milk yield, selection on M3 or EI₃ achieved the greatest genetic response, whereas selection on EI₁ produced the largest genetic progress per day. In terms of total net merit, selection on I₃ brought the largest response, whereas selection EI₁ yielded the greatest genetic progress per day. A multiple-lactation random regression test-day model simultaneously yields the EBV of the 3 lactations for all animals included in the analysis even though the younger animals do not have the opportunity to complete the first 3 lactations. It is important to use the first 3 lactation EBV for selection decision rather than only the first lactation EBV in spite of the fact that the first-parity selection criteria achieved a faster genetic progress per day than the 3-parity selection criteria. Under a multiple-lactation random regression animal model analysis, the use of the first 3 lactation EBV for selection decision does not prolong the generation interval as compared with the use of only the first lactation EBV. Thus, it is justified to compare genetic response on a lifetime basis rather than on a per-day basis. The results suggest the use of M3 or EI₃ for genetic improvement of total milk yield and the use of I₃ for genetic improvement of total net merit H. Although this study deals with selection for

3-parity milk production, the same principle applies to selection for lifetime milk production.

Key words: total milk yield, total persistency, eigen index, selection index

INTRODUCTION

Because of high replacement costs of dairy cows, dairy producers strive to keep their cows in the herds as long as possible and thus are interested in lifetime milk production of dairy cows. Although efficient lifetime milk production is vitally important to the dairy industry, literature reports on this issue are relatively meager. Lactation persistency commonly refers to the rate of decline after peak yield. Given a fixed total lactation yield, a cow with a flatter curve is said to be more persistent. A persistent cow has better use of cheap roughage, suffers less stress from high peak yield, is more resistant to disease, and is more profitable (Gengler, 1996; Swalve and Gengler, 1999). Therefore, it makes good economic sense to improve lifetime performance in lactational milk and persistency.

Methods of estimating the genetic and phenotypic parameters in Holstein cows change with technical progress in statistical methodologies. The genetic parameters of lifetime production traits have been estimated using daughter-dam regression (Hargrove et al., 1969), least squares analysis (Miller et al., 1967; Hoque and Hodges, 1980), multivariate REML (Chauhan et al., 1992; Jairath et al., 1994, 1995; Zarnecki and Morek-Kopec, 2006), and multivariate random regression (RR) analysis (Togashi et al., 2007). High genetic correlation between first lactation milk and lifetime production have led to the conclusion that selection on early lactation yield is effective for improving lifetime production (Hoque and Hodges, 1980; Jairath et al., 1994, 1995). The literature reports on selection for lifetime performance in dairy cattle are scant because of extra costs and time required for data collection as compared with selection based only on first lactation. Theoretical efficiency of different selection methods based on early performance traits has been compared in terms

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of lifetime profit (Lin and Allaire, 1977) and in terms of total milk yield to 48, 72, or 84 mo of age in Holstein cows (Lin and Allaire, 1978). Canadian national genetic evaluation is based on a 3-lactation, 4-trait RR test-day (TD) model to estimate the breeding values of milk, fat, and protein yields and SCS for each lactation (Schaeffer et al., 2000). The EBV of various traits were in turn combined to form the lifetime profit index. The purposes of this study were 2-fold: 1) to evaluate the efficiency of a set of 6 selection criteria for improving the first 3-lactation total milk yield and 2) to compare a second set of 9 different selection criteria for improving the net merit comprising 3-lactation total milk yield and total lactation persistency. The comparison of the efficiency of different selection criteria was investigated in terms of total genetic progress for the first 3 lactations and in terms of genetic progress per unit of time.

MATERIALS AND METHODS

The genetic parameters used for this study were obtained from the analysis of the Japanese Holstein cows (Togashi et al., 2007) using a multiple-lactation RR TD model with a cubic Legendre polynomial (LP) and with the use of the relationship matrix among animals to account for the effect of selection. Briefly, the data consisted of 238,719 TD milk yields of the first 3 lactations from 1996 to 2000. Only completed lactations were used to avoid any implicit interpolation or extrapolation in the model as suggested by Pool et al. (2000). A complete lactation was considered to have at least 305 DIM after parturition. To obtain a more informative data set (Pool and Meuwissen, 2000), all lactations of the first 3 parities were required to have a minimum of 10 TD records, and the number of cows per herd-test-date was required to have a minimum of 7. The 3-parity RR TD model fitted with cubic LP produced a (12×1) vector (α) of the additive genetic RR coefficients with an (12×12) additive genetic RR covariance matrix $\mathbf{K}$ and a (301×12) LP coefficient matrix Φ :

$$\alpha = \begin{bmatrix} \alpha_{(1)} \\ \alpha_{(2)} \\ \alpha_{(3)} \end{bmatrix}; \text{Var}(\alpha) = \begin{bmatrix} \mathbf{K}_{11} & \mathbf{K}_{12} & \mathbf{K}_{13} \\ \mathbf{K}_{21} & \mathbf{K}_{22} & \mathbf{K}_{23} \\ \mathbf{K}_{31} & \mathbf{K}_{32} & \mathbf{K}_{33} \end{bmatrix} \text{ and } \Phi = [\Phi_{(1)} \quad \Phi_{(2)} \quad \Phi_{(3)}],$$

where $\alpha_{(i)}$ = a (4×1) vector of the additive genetic RR coefficients that apply to individual animals of the i th lactation, and $\Phi_{(i)}$ = the (301×4) LP coefficient matrix of the i th lactation, which is the same for the 3 lactations. The diagonal blocks ($\mathbf{K}_{11}$, $\mathbf{K}_{22}$, and $\mathbf{K}_{33}$) of the

matrix $\mathbf{K}$ are the additive genetic RR coefficient covariance matrices within parity, and the off-diagonal blocks are the additive genetic RR coefficient covariance matrices between parities. The EBV of the daily yields from DIM 5 to 305 of the i th lactation are $\Phi_{(i)}\alpha_{(i)}$, and the EBV of the i th lactation is $\mathbf{1}'\Phi_{(i)}\alpha_{(i)}$, where $\mathbf{1}$ = a summing vector. Throughout the text, the subscript “ i ” in parenthesis refers to the number of lactations.

For ease of reference, the following notations will be used hereafter: $M_{(i)}$ = i th-parity milk EBV ($i = 1$ to 3); $M1 = \sum_{i=1}^1 M_{(i)}$ (i.e., first-parity milk EBV); $M2 = \sum_{i=1}^2 M_{(i)}$ (i.e., first 2-parity milk EBV); $M3 = \sum_{i=1}^3 M_{(i)}$ (i.e., first 3-parity milk EBV). Similarly, $P_{(i)}$ = the i th-parity persistency EBV, and $P1$, $P2$, and $P3$ = the first-parity, first 2-parity, and first 3-parity persistency EBV, respectively, where lactation persistency was measured as the difference between EBV at 280 DIM and peak DIM. Genetic responses in milk yield and lactation persistency of the i th lactation are denoted as $\Delta G_{(i)}$ and $\Delta P_{(i)}$, respectively. The 3-lactation total milk yield and total persistency will be simply referred to as total milk yield and total lactation persistency, respectively.

Selection for Improvement of Total Milk Yield

Selection for genetic improvement of total milk yield considers 2 sets of relative economic weights among the first 3 lactations: $a_1 : a_2 : a_3 = 1:1:1$ and $a_1 : a_2 : a_3 = 1.1:1.05:1$, with a_i being the relative economic weight of the i th lactation milk. Consequently, this yields 2 breeding goals: $H^{(1)} = g_{(1)} + g_{(2)} + g_{(3)}$ and $H^{(2)} = 1.1g_{(1)} + 1.05g_{(2)} + g_{(3)}$, where $g_{(i)}$ = the genetic value of the i th lactation milk ($i = 1, 2$, or 3) and the superscript “ j ” of H refers to the j th breeding goal ($j = 1$ or 2). Six selection criteria for improving total milk yield (Table 1) were compared: 1) $M1$, 2) $M2$, 3) $M3$, 4) first-parity eigen index EI_1 based on the 4 eigenvectors of $\mathbf{K}_{11}$, 5) first 2-parity eigen index EI_2 based on the 8 eigenvectors of the submatrix of $\mathbf{K}$ corresponding to the first 2 lactations, and 6) first 3-parity eigen index EI_3 based on the 12 eigenvectors of the matrix $\mathbf{K}$. These eigen indices were derived using a maximization procedure, which is detailed in the derivation of eigen indices section.

Selection for Net Merit Comprising Total Milk Yield and Total Persistency

Let the vectors $\Phi_{280(i)}$ and $\Phi_{peak(i)}$ contain the rows of the LP coefficient matrix (Φ) corresponding to DIM 280 and peak DIM of the i th lactation. Let $g_{280(i)}$ and $g_{peak(i)}$ be the genetic values of the daily yields at DIM 280

Table 1. A summary of selection goals (H) and selection criteria compared in this study¹

Selection goals (H)	$a_1 : a_2 : a_3$	$w_m : w_p$	Selection criteria compared
$H^{(1)} = g_{(1)} + g_{(2)} + g_{(3)}$	1:1:1		M1, M2 ⁽¹⁾ , M3 ⁽¹⁾ , EI ₁ ⁽¹⁾ , EI ₂ ⁽¹⁾ , EI ₃ ⁽¹⁾
$H^{(2)} = 1.1g_{(1)} + 1.05g_{(2)} + g_{(3)}$	1.1:1.05:1		M1, M2 ⁽²⁾ , M3 ⁽²⁾ , EI ₁ ⁽²⁾ , EI ₂ ⁽²⁾ , EI ₃ ⁽²⁾
$H^{(3)} = \sum_{i=1}^3 g_{(i)}^* + \sum_{i=1}^3 p_{(i)}$	1:1:1	1:1	M1, M2 ⁽³⁾ , M3 ⁽³⁾ , EI ₁ ⁽³⁾ , EI ₂ ⁽³⁾ , EI ₃ ⁽³⁾ , I ₁ ⁽³⁾ , I ₂ ⁽³⁾ , I ₃ ⁽³⁾
$H^{(4)} = 1.1g_{(1)}^* + 1.05g_{(2)}^* + g_{(3)}^* + \sum_{i=1}^3 p_{(i)}$	1.1:1.05:1	1:1	M1, M2 ⁽⁴⁾ , M3 ⁽⁴⁾ , EI ₁ ⁽⁴⁾ , EI ₂ ⁽⁴⁾ , EI ₃ ⁽⁴⁾ , I ₁ ⁽⁴⁾ , I ₂ ⁽⁴⁾ , I ₃ ⁽⁴⁾
$H^{(5)} = \sum_{i=1}^3 g_{(i)}^* + 50 \sum_{i=1}^3 p_{(i)}$	1:1:1	1:50	M1, M2 ⁽⁵⁾ , M3 ⁽⁵⁾ , EI ₁ ⁽⁵⁾ , EI ₂ ⁽⁵⁾ , EI ₃ ⁽⁵⁾ , I ₁ ⁽⁵⁾ , I ₂ ⁽⁵⁾ , I ₃ ⁽⁵⁾
$H^{(6)} = 1.1g_{(1)}^* + 1.05g_{(2)}^* + g_{(3)}^* + 50 \sum_{i=1}^3 p_{(i)}$	1.1:1.05:1	1:50	M1, M2 ⁽⁶⁾ , M3 ⁽⁶⁾ , EI ₁ ⁽⁶⁾ , EI ₂ ⁽⁶⁾ , EI ₃ ⁽⁶⁾ , I ₁ ⁽⁶⁾ , I ₂ ⁽⁶⁾ , I ₃ ⁽⁶⁾

¹ $g_{(i)}$ = genetic value of the i th lactation milk ($i = 1, 2, 3$); $g_{(i)}^*$ = $g_{(i)}$ minus genetic values at DIM 280 and DIM peak; $a_1 : a_2 : a_3$ = relative economic weights of the 3 lactation milk yields; $w_m : w_p$ = relative economic weights between total milk yield and total persistency; M1 = first-parity EBV; M2^(j) or M3^(j) = 2- or 3-parity milk EBV weighted by economic weights of the lactation milk. Eigen indexes EI₁^(j), EI₂^(j), and EI₃^(j) and selection indexes I₁^(j), I₂^(j), and I₃^(j) are derived to maximize genetic response in selection goal $H^{(j)}$ ($j = 1$ to 6).

and DIM peak of the i th lactation, respectively. The genetic value of persistency of the i th lactation was defined as $p_{(i)} = g_{280(i)} - g_{peak(i)}$. The estimate of $p_{(i)}$ is $\hat{p}_{(i)} = [\Phi_{280(i)} - \Phi_{peak(i)}]\alpha_{(i)} = \Phi_{d(i)}\alpha_{(i)}$, where $\Phi_{d(i)} = \Phi_{280(i)} - \Phi_{peak(i)}$. Let $g_{(i)}^*$ be the genetic value of the i th lactation milk yield excluding $g_{280(i)}$ and $g_{peak(i)}$. The exclusion of g_{280} and g_{peak} is to avoid duplication between lactation milk and persistency measure. Inclusion of g_{280} and g_{peak} in net merit would mean that maximizing the correlation between the index and net merit in the derivation of the index would increase both g_{280} and g_{peak} separately and their difference $g_{280} - g_{peak}$ (i.e., persistency measure) at the same time. This would be an offsetting, contradictory process. Let $\Phi_{(i)}^*$ be a (299×4) submatrix of $\Phi_{(i)}$ by deleting the rows corresponding to DIM 280 and DIM peak. Thus, the estimate of $g_{(i)}^*$ is $g_{(i)}^* = \mathbf{1}'\Phi_{(i)}^*\alpha_{(i)}$.

Let w_m and w_p be the relative economic weights between total milk yield and total persistency. The net merit (selection goal) comprising total milk yield and total persistency take a general form of $H = w_m \sum_{i=1}^3 a_i g_{(i)}^* + w_p \sum_{i=1}^3 p_{(i)}$. This study considers 2 sets of relative economic weights between total milk yield and total persistency ($w_m : w_p = 1:1$ and $w_m : w_p = 1:50$) and 2 sets of relative economic weights among the 3 lactation milks ($a_1 : a_2 : a_3 = 1:1:1$ and $a_1 : a_2 : a_3 = 1.1:1.05:1$), thus yielding 4 selection goals: $H^{(3)}$, $H^{(4)}$, $H^{(5)}$, and $H^{(6)}$. All combinations of selection goals and selection criteria studied are summarized in Table 1. The first-, 2-, and 3-parity eigen indices (EI₁^(j), EI₂^(j), EI₃^(j)) and selection indices (I₁^(j), I₂^(j), and I₃^(j)) were derived

to maximize the selection goal $H^{(j)}$, where $j = 1$ to 6. For example, when $j = 4$, each of the selection criteria EI₁⁽⁴⁾, EI₂⁽⁴⁾, EI₃⁽⁴⁾, I₁⁽⁴⁾, I₂⁽⁴⁾, and I₃⁽⁴⁾ is derived by maximizing its correlation with selection goal $H^{(4)}$ (Table 1). By dropping the superscript “j,” the first-, 2-, and 3-parity selection indices (I₁^(j), I₂^(j), and I₃^(j)) take the general form of $I_1 = b_1M_{(1)} + b_2P_{(1)}$, $I_2 = b_1M_{(1)} + b_2M_{(2)} + b_3P_{(1)} + b_4P_{(2)}$, and $I_3 = b_1M_{(1)} + b_2M_{(2)} + b_3M_{(3)} + b_4P_{(1)} + b_5P_{(2)} + b_6P_{(3)}$, respectively, where b_i = the index weight. The relative economic weights between total milk and total persistency ($w_m : w_p$) are arbitrarily chosen, because no literature reports are available. Collard et al. (1999) estimated the relative economic weights to be 1.46:1.02:0.60 for protein EBV of the first 3 lactations as compared with 0.41:0.33:0.26 for production EBV or persistency of the first 3 lactations (NRS, 2002).

Derivation of Eigen Indices. The procedures for constructing various eigen indices were given in Togashi and Lin (2006). The construction of the first-parity eigen index based on the 4 eigenvectors of $\mathbf{K}_{11}$ is given below as an example. The same principle applies to the construction of the 2- or 3-parity eigen indices.

The first-parity eigen index is $EI_1 = \sum_{j=1}^4 b_j(\mathbf{e}_j'\alpha_{(1)}) = (\mathbf{E}_4'\alpha_{(1)})'\mathbf{b}$, where $\mathbf{e}_j$ = the j th eigenvector of $\mathbf{K}_{11}$, the matrix $\mathbf{E}_4$ contains the 4 eigenvectors of $\mathbf{K}_{11}$ column-wise, and $\alpha_{(1)}$ is as defined above. By index theory, maximizing the correlation between EI₁ and the net merit $H = w_m \sum_{i=1}^3 a_i g_{(i)}^* + w_p \sum_{i=1}^3 p_{(i)}$ leads to the following index equations:

$$\text{Var}(\mathbf{E}'_4 \alpha_{(1)}) \mathbf{b} = \text{Cov}(\mathbf{E}'_4 \alpha_{(1)}, w_m \sum_{i=1}^3 a_i g^*_{(i)}) \\ + \text{Cov}(\mathbf{E}'_4 \alpha_{(1)}, w_p \sum_{i=1}^3 p_{(i)}).$$

This set of index equations is equivalent to:

$$\mathbf{E}'_4 \mathbf{K}_{11} \mathbf{E}_4 \mathbf{b} = w_m \sum_{i=1}^3 a_i \mathbf{E}'_4 \mathbf{K}_{1i} \Phi^*_{(i)} \mathbf{1} + w_p \sum_{i=1}^3 \mathbf{E}'_4 \mathbf{K}_{1i} \Phi'_{d(i)}.$$

Because $\mathbf{E}'_4 \mathbf{K}_{11} \mathbf{E}_4 = \mathbf{D}_4$, where $\mathbf{D}_4$ is a (4×4) diagonal matrix with the 4 eigenvalues of $\mathbf{K}_{11}$ on the diagonal, it follows that $\mathbf{b} = \mathbf{D}_4^{-1} \left(w_m \sum_{i=1}^3 a_i \mathbf{E}'_4 \mathbf{K}_{1i} \Phi^*_{(i)} \mathbf{1} + w_p \sum_{i=1}^3 \mathbf{E}'_4 \mathbf{K}_{1i} \Phi'_{d(i)} \right)$. In comparison, maximizing the correlation between EI_1 and total milk yield would result in $\mathbf{b} = \mathbf{D}_4^{-1} \left(\sum_{i=1}^3 a_i \mathbf{E}'_4 \mathbf{K}_{1i} \Phi'_{(i)} \mathbf{1} \right)$.

The genetic responses in daily yields from DIM 5 to 305 of the i th lactation due to selection on EI_1 are:

$$\underline{\Delta}_{(i)} = \frac{\text{Cov}(\Phi_{(i)} \alpha_{(i)}, \alpha'_{(1)} \mathbf{E}_4 \mathbf{b})}{\sigma_{\text{EI}_1}^2} (\text{SD}) = \Phi_{(i)} \mathbf{K}_{i1} \mathbf{E}_4 \mathbf{b} \left(\frac{\bar{i}}{\sigma_{\text{EI}_1}} \right),$$

where $\sigma_{\text{EI}_1} = \sqrt{\mathbf{b}' \mathbf{E}'_4 \mathbf{K}_{11} \mathbf{E}_4 \mathbf{b}}$, which is the square root of the product of the solution vector $\mathbf{b}'$ and the left-hand side of the index equations, SD = the selection differential, and $\bar{i}$ = the selection intensity.

Derivation of Selection Indices. The derivation of the first 2-parity selection index I_2 is given below as an example. The same principle applies to the derivation of I_1 and I_3 . The selection index I_2 is based on milk EBV and persistency EBV of the first 2 lactations:

$$\text{I}_2 = b_1 \hat{g}^*_{(1)} + b_2 \hat{g}^*_{(2)} + b_3 \hat{p}_{(1)} + b_4 \hat{p}_{(2)},$$

where $\hat{g}^*_{(i)}$ and $\hat{p}_{(i)}$ = the estimates of $g^*_{(i)}$ and $p_{(i)}$, respectively ($i = 1, 2$), as defined above.

According to index theory, maximizing the correlation between I_2 and H results in the following set of index equations:

$$\begin{bmatrix} \text{Var}(\hat{g}^*_{(1)}) & \text{Cov}(\hat{g}^*_{(1)}, \hat{g}^*_{(2)}) & \text{Cov}(\hat{g}^*_{(1)}, \hat{p}_{(1)}) & \text{Cov}(\hat{g}^*_{(1)}, \hat{p}_{(2)}) \\ \text{Symmetric} & \text{Var}(\hat{g}^*_{(2)}) & \text{Cov}(\hat{g}^*_{(2)}, \hat{p}_{(1)}) & \text{Cov}(\hat{g}^*_{(2)}, \hat{p}_{(2)}) \\ & & \text{Var}(\hat{p}_{(1)}) & \text{Cov}(\hat{p}_{(1)}, \hat{p}_{(2)}) \\ & & & \text{Var}(\hat{p}_{(2)}) \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} =$$

$$\begin{bmatrix} \text{Cov}\left(\hat{g}^*_{(1)}, \sum_{i=1}^3 a_i g^*_{(i)}\right) & \text{Cov}\left(\hat{g}^*_{(1)}, \sum_{i=1}^3 p_{(i)}\right) \\ \text{Cov}\left(\hat{g}^*_{(2)}, \sum_{i=1}^3 a_i g^*_{(i)}\right) & \text{Cov}\left(\hat{g}^*_{(2)}, \sum_{i=1}^3 p_{(i)}\right) \\ \text{Cov}\left(\hat{p}_{(1)}, \sum_{i=1}^3 a_i g^*_{(i)}\right) & \text{Cov}\left(\hat{p}_{(1)}, \sum_{i=1}^3 p_{(i)}\right) \\ \text{Cov}\left(\hat{p}_{(2)}, \sum_{i=1}^3 a_i g^*_{(i)}\right) & \text{Cov}\left(\hat{p}_{(2)}, \sum_{i=1}^3 p_{(i)}\right) \end{bmatrix} \begin{bmatrix} w_m \\ w_p \end{bmatrix}.$$

Computationally, this set of equations can be rewritten as,

$$\begin{bmatrix} \mathbf{1}' \Phi^*_{(1)} \mathbf{K}_{11} \Phi^*_{(1)} \mathbf{1} & \mathbf{1}' \Phi^*_{(1)} \mathbf{K}_{12} \Phi^*_{(2)} \mathbf{1} & \mathbf{1}' \Phi^*_{(1)} \mathbf{K}_{11} \Phi'_{d(1)} \mathbf{1} & \mathbf{1}' \Phi^*_{(1)} \mathbf{K}_{12} \Phi'_{d(2)} \mathbf{1} \\ \text{Symmetric} & \mathbf{1}' \Phi^*_{(2)} \mathbf{K}_{22} \Phi^*_{(2)} \mathbf{1} & \mathbf{1}' \Phi^*_{(2)} \mathbf{K}_{21} \Phi'_{d(1)} \mathbf{1} & \mathbf{1}' \Phi^*_{(2)} \mathbf{K}_{22} \Phi'_{d(2)} \mathbf{1} \\ & & \Phi_{d(1)} \mathbf{K}_{11} \Phi'_{d(1)} & \Phi_{d(1)} \mathbf{K}_{12} \Phi'_{d(2)} \\ & & & \Phi_{d(2)} \mathbf{K}_{22} \Phi'_{d(2)} \end{bmatrix}$$

$$\begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} = \begin{bmatrix} \sum_{i=1}^3 a_i \mathbf{1}' \Phi^*_{(1)} \mathbf{K}_{1i} \Phi^*_{(i)} \mathbf{1} & \sum_{i=1}^3 \mathbf{1}' \Phi^*_{(1)} \mathbf{K}_{1i} \Phi'_{d(i)} \mathbf{1} \\ \sum_{i=1}^3 a_i \mathbf{1}' \Phi^*_{(2)} \mathbf{K}_{2i} \Phi^*_{(i)} \mathbf{1} & \sum_{i=1}^3 \mathbf{1}' \Phi^*_{(2)} \mathbf{K}_{2i} \Phi'_{d(i)} \mathbf{1} \\ \sum_{i=1}^3 a_i \Phi_{d(1)} \mathbf{K}_{1i} \Phi^*_{(i)} \mathbf{1} & \sum_{i=1}^3 \Phi_{d(1)} \mathbf{K}_{1i} \Phi'_{d(i)} \mathbf{1} \\ \sum_{i=1}^3 a_i \Phi_{d(2)} \mathbf{K}_{2i} \Phi^*_{(i)} \mathbf{1} & \sum_{i=1}^3 \Phi_{d(2)} \mathbf{K}_{2i} \Phi'_{d(i)} \mathbf{1} \end{bmatrix} \begin{bmatrix} w_m \\ w_p \end{bmatrix},$$

where vector $\Phi_{d(i)}$ ($i = 1, 2$) was as defined previously. Daily genetic responses in milk ($\underline{\Delta}_{(i)}$) from d 5 to 305 of the i th lactation due to selection on I_2 are:

$$\underline{\Delta}_{(i)} = \text{Cov}(\Phi_{(i)} \alpha_{(i)}, \text{I}_2) (\bar{i} / \sigma_{\text{I}_2}) =$$

$$\left\{ \sum_{j=1}^2 \Phi_{(i)} \mathbf{K}_{ij} \Phi^*_{(j)} \mathbf{1} b_j + \sum_{j=1}^2 \Phi_{(i)} \mathbf{K}_{ij} \Phi'_{d(j)} b_{(j+2)} \right\} (\bar{i} / \sigma_{\text{I}_2}),$$

where σ_{I_2} = the standard deviation of the index I_2 , which is equal to the square root of the product of the solution vector and the left-hand side of the index equations. The genetic response for the i th lactation milk is $\Delta \text{G}_{(i)} = \mathbf{1}' \underline{\Delta}_{(i)}$. Let $\Delta_{280(i)}$ and $\Delta_{\text{peak}(i)}$ be daily genetic responses at DIM 280 and DIM peak of the i th lactation, respectively. The genetic response for the i th lactation milk

Table 2. Comparison of selection criteria for genetic improvement of total milk yield¹

Selection goal $H^{(j)}$	Genetic response	Selection criteria					
		M1	M2 ^(j)	M3 ^(j)	EI ₁ ^(j)	EI ₂ ^(j)	EI ₃ ^(j)
$j = 1$	$\Delta G_{(1)}$	848.2	840.2	836.5	846.4	842.2	835.9
	$\Delta G_{(2)}$	1,234.4	1,262.3	1,247.2	1,239.3	1,255.6	1,247.5
	$\Delta G_{(3)}$	1,140.1	1,136.0	1,184.0	1,144.1	1,147.9	1,184.2
	$\Delta H^{(1)}$	3,222.7	3,238.5	3,267.7	3,229.8	3,245.7	3,267.6
	$\Delta H^{(1)}/N_d$	2.888	2.093	1.645	2.894	2.097	1.645
$j = 2$	$\Delta H^{(2)}$	3,369.2	3,385.9	3,413.7	3,376.4	3,392.8	3,413.8
	$\Delta H^{(2)}/N_d$	3.019	2.188	1.718	3.026	2.192	1.718

¹ $\Delta G_{(i)}$ = genetic response for the i th lactation milk; $\Delta H^{(j)}$ = genetic response in the j th selection goal ($j = 1$ or 2); N_d = days from birth to 305 d of the i th lactation for i th parity-based selection criteria: $N_d = 1,116$ d for M1 and EI₁; $N_d = 1,548$ d for M2 and EI₂; $N_d = 1,987$ d for M3 and EI₃. Notations for M1, M2, M3, EI₁, EI₂, and EI₃ were summarized in Table 1.

excluding daily responses at DIM 280 and DIM peak is $\Delta G_{(i)}^* = \Delta G_{(i)} - (\Delta_{280(i)} + \Delta_{peak(i)})$. The genetic response for the i th lactation persistency is $\Delta P_{(i)} = \Delta_{280(i)} - \Delta_{peak(i)}$. The genetic response in net merit is $\Delta H = w_m \sum_{i=1}^3 a_i \Delta G_{(i)}^* + w_p \sum_{i=1}^3 \Delta P_{(i)}$. Alternatively, ΔH due to selection on I_2 can be computed as $\Delta H = \bar{i} \sigma_{I_2}$, where selection intensity $\bar{i}$ is set to unity for all selection criteria compared.

RESULTS AND DISCUSSION

Different selection criteria involved different length of production periods for their construction and application. It makes sense to compare different selection criteria in terms of genetic progress per day. The number of days (N_d) used to compute genetic progress per day is 1,116 d from birth to 305 d of the first lactation for first parity-based selection criteria M1, EI₁, and I₁; 1,548 d from birth to 305 d of the second lactation for the first 2-parity-based criteria M2, EI₂, and I₂; and 1,987 d from birth to 305 d of the third lactation for the 3-parity-based criteria M3, EI₃, and I₃. The length from birth to 305 d of the first, second, and third lactation was computed for each cow and then averaged to obtain the average number of days for computing genetic progress per day.

Genetic Responses to Selection for Total Milk Yield

The genetic response to selection for total milk yield of the first 3 lactations weighted by $a_1 : a_2 : a_3 = 1:1:1$ and $a_1 : a_2 : a_3 = 1.1:1.05:1$ is shown in Table 2. Selection on first-parity milk EBV (M1) produced the greatest genetic gain in the first lactation milk, selection on the first 2-parity milk EBV (M2) yielded the greatest

response in the second lactation milk, and selection on first 3-parity milk EBV (M3) brought the greatest genetic response in the third lactation milk (Table 2). Because lactation yield increases as the number of lactations increases, the third lactation EBV is expected to constitute a larger proportion of the 3-parity total EBV than the first or the second lactation EBV. Thus, selection on the 3-parity total EBV would produce a larger response in the third lactation yield than in the first and the second lactation yields. Selection on M3 is equivalent to selection on EI₃ in terms of total genetic gain (ΔH) or genetic progress per day ($\Delta H/N_d$) whether $a_1 : a_2 : a_3 = 1:1:1$ or $a_1 : a_2 : a_3 = 1.1:1.05:1$ (Table 2). It makes no difference to weigh the 3 lactations under this situation.

Table 2 shows that selection on M3 or EI₃ produced the greatest genetic gain in total milk yield, but yielded the smallest genetic progress per day. Of the 6 selection criteria compared, EI₁ resulted in the fastest genetic progress per day regardless of the economic weight among the 3 lactations (Table 2). Although selection on M1 produced the smallest genetic gain in total milk yield, it yielded a much faster genetic progress per day than selection on M2 or M3. In terms of genetic progress on a per-day basis ($\Delta H/N_d$), the denominator N_d plays a more important role than the numerator ΔH in determining the value of a ratio. For example, selection on M1 achieved a faster genetic progress on a per-day basis than selection on M3, primarily because the denominator N_d for M1 is much smaller than for M3 (1,116 vs. 1,987 d).

Genetic Responses to Selection for Net Merit (H) Comprising Total Milk Yield and Total Persistency

The genetic responses to the 9 selection criteria compared (M1, M2, M3, EI₁, EI₂, EI₃, I₁, I₂, and I₃) were

Table 3. Comparison of selection criteria for genetic improvement of total net merit comprising total milk yield and total persistency¹

Selection goal $H^{(j)}$	Genetic response	Selection criteria								
		M1	M2 ^(j)	M3 ^(j)	EI ₁ ^(j)	EI ₂ ^(j)	EI ₃ ^(j)	I ₁ ^(j)	I ₂ ^(j)	I ₃ ^(j)
$j = 3$	$\Delta H^{(3)}$	3,204.2	3,219.9	3,249.2	3,211.7	3,227.5	3,249.2	3,178.5	3,221.8	3,249.9
	$\Delta H^{(3)}/N_d$	2.872	2.081	1.635	2.878	2.085	1.635	2.848	2.082	1.636
$j = 4$	$\Delta H^{(4)}$	3,349.8	3,366.1	3,394.3	3,357.4	3,373.7	3,394.3	3,322.4	3,368.0	3,395.1
	$\Delta H^{(4)}/N_d$	3.002	2.175	1.708	3.009	2.180	1.708	2.977	2.176	1.709
$j = 5$	$\Delta H^{(5)}$	3,297.6	3,312.3	3,356.8	3,351.1	3,376.6	3,396.4	3,317.7	3,391.0	3,433.4
	$\Delta H^{(5)}/N_d$	2.955	2.140	1.689	3.003	2.182	1.709	2.973	2.191	1.728
$j = 6$	$\Delta H^{(6)}$	3,443.2	3,458.8	3,501.3	3,495.5	3,520.4	3,539.3	3,460.3	3,534.9	3,575.4
	$\Delta H^{(6)}/N_d$	3.086	2.235	1.762	3.133	2.275	1.781	3.101	2.284	1.800

¹ $\Delta H^{(j)}$ = genetic response in selection goal H ($j = 3$ to 6); N_d = days from birth to 305 d of the i th lactation for i th parity-based selection criteria: $N_d = 1,116$ d for M1 and EI₁; $N_d = 1,548$ d for M2 and EI₂; $N_d = 1,987$ d for M3 and EI₃. Notations for M1, M2, M3, EI₁, EI₂, EI₃, I₁, I₂, and I₃ were summarized in Table 1.

given in Table 3 for different combinations of relative economic weights between total milk yield and total persistency ($w_m : w_p = 1:1$ and $w_m : w_p = 1:50$) and among the 3 lactation milks ($a_1 : a_2 : a_3 = 1:1:1$ and $a_1 : a_2 : a_3 = 1.1:1.05:1$). This table consistently showed that selection on I₃ produced the largest response in net merit (ΔH), while selection on eigen index EI₁ yielded the fastest genetic progress per day ($\Delta H/N_d$). Of the 9 selection criteria compared, selection on I₃ consistently produced the greatest correlated response in total milk yield excluding the daily response at DIM 280 and DIM peak ($\sum_{i=1}^3 \Delta G_{(i)}^*$, Table 3). For a given set

of relative economic weights of the 3 lactations, the superiority of I₃ in terms of ΔH increased as w_p/w_m increased (Table 3). This indicates the importance of going through maximization procedure to derive the selection criteria when a great difference exists between w_p and w_m . The possible reasons for the advantages of I₃ and EI₁ over the other criteria compared are as follows: 1) the index traits of I₃ are equivalent to the component traits of the net merit; 2) the construction of both eigen and selection indices takes into account the relative economic weights among the 3 parities and between total milk yield and total persistency; and 3) the construction of both eigen and selection indices has maximized their correlation with total milk yield or total net merit H, whereas selection criterion M1, M2, or M3 does not require the maximization process so that their correlation with total milk yield or total net merit H is not at a maximum.

Hoque and Hodges (1980) reported that selection on first lactation milk was an effective means of maximizing lifetime milk, because a high genetic correlation of 0.56 was found between first lactation milk and lifetime milk. Heritability estimates of lifetime milk, fat, and protein yields were very low, ranging from 0.02 to 0.07 (Chauhan et al., 1992; Jairath et al., 1994;

Zarnecki and Morek-Kopec, 2006), suggesting that direct selection for lifetime milk would not be effective. These reports are somewhat contradictory, because if direct selection on lifetime milk is ineffective in raising lifetime production, it is highly unlikely that indirect selection on first lactation milk yield would be effective for improving lifetime milk yield. There should be no surprise to find a high correlation between first lactation milk and lifetime milk because of a part-whole correlation. Under single-trait analysis, the estimation of heritability of and correlation between first lactation yield and lifetime milk production requires the accumulation of milk yields across lactation over lifetime. Lifetime milk production is a complex trait highly affected by a wide range of environmental and management factors on top of genetics. More importantly, these environmental and management factors could vary from day to day or from animal to animal over a lifetime, thus resulting in a low heritability of lifetime milk production traits as reported in literature. If all of these important factors are not properly accounted for, the genetic and phenotypic estimates of cumulative lifetime milk production traits would be grossly inaccurate and thus produce misleading results about genetic improvement of lifetime milk production.

This study has 3 advantages over the literature reports about the comparison of different selection criteria for lifetime production. First, the genetic parameters used in this study were based on a multiple-lactation RR animal model, which takes into account the environmental and management variations of the first 3 lactations on a TD basis. Second, this study demonstrates that both phenotypic and genetic estimates of the cumulative lifetime production are not necessary for computing genetic progress in lifetime production from different selection criteria compared, thus eliminating the need to compute the cumulative lifetime

production and greatly reducing the estimation errors. Third, under a multiple-lactation RR TD animal model, EBV are produced for all animals and all lactations with a greater reliability. These 3 desirable features of the multiple-lactation RR TD animal model analysis used in this study are expected to produce more accurate results than a single-trait animal model analysis of the cumulative lactation production reported in the literature.

The multiple-lactation RR animal model simultaneously yields the EBV for all lactations and all animals including the censored data or the younger animals that do not have the opportunity to complete the 3 lactations. Therefore, selection based on the first 3 lactation EBV does not prolong the generation interval as compared with selection solely on first lactation EBV that ignores the second and third lactation EBV. Because the first 3 lactation EBV for all animals are simultaneously generated in genetic evaluation, all of the 3 lactation EBV should be used subsequently to make selection decision in spite of the fact that the first-parity selection criteria is more efficient than the 3-parity selection criteria in terms of genetic progress per day. The genetic response in terms of total milk yield or total net merit is more important than in terms of genetic progress per day.

Due to the results of this study, selection for total milk yield should be based on M3 or EI_3 (Table 2), and selection for total net merit comprising total milk yield and total persistency should be based on 3-parity selection index I_3 (Table 3). The advantage of the selection index I_3 in terms of net merit arises from the maximization of the correlation between I_3 and net merit (H). In comparison, the conventional practice of combining the EBV of various traits for selection purpose did not go through such a maximization procedure. The benefit of going through the maximization process to derive a selection criterion is more apparent when the selection criterion and the net merit do not contain the same number of traits.

Among the 3 early selection criteria based on the first lactation EBV ($M1$, EI_1 , and I_1), selection on EI_1 is more efficient than $M1$ and I_1 in terms of total genetic response or genetic progress per day (Tables 2 and 3). Therefore, if only first lactation milk is available for genetic evaluation using a single-trait RR animal model, the eigen index EI_1 is the method of choice for genetic improvement of total milk yield or total net merit.

CONCLUSIONS

In a multilactation evaluation, selection based on the first 3 lactation EBV does not prolong the genera-

tion interval as compared with selection solely on the first lactation EBV that disregards the second and the third lactation EBV. It is important to simultaneously utilize the first 3 lactation EBV to improve total performance. The results of this study indicate that selection criterion of choice depends upon selection goal. To improve total milk yield of the first 3 lactations, the selection method of choice is 3-parity eigen index (EI_3) or 3-parity milk EBV ($M3$). To improve net merit comprising total milk yield and total lactation persistency, the selection method of choice is 3-parity selection index I_3 . This is due to the fact that the selection index I_3 is derived maximizing the correlation between I_3 and net merit. In contrast, conventional practice of combining the EBV of various traits for selection purpose did not go through maximization procedure. However, if only first lactation EBV is available for early selection, the first-parity eigen index EI_1 is more effective than the first-parity selection index I_1 or selection on first lactation EBV in terms of total milk yield, total net merit, or genetic progress per day.

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