Lactation Persistency as a Component Trait of the Selection Index and Increase in Reliability by Using Single Nucleotide Polymorphism in Net Merit Defined as the First Five Lactation Milk Yields and Herd Life

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ABSTRACT: We first sought to clarify the effects of discounted rate, survival rate, and lactation persistency as a component trait of the selection index on net merit, defined as the first five lactation milks and herd life (HL) weighted by 1 and 0.389 (currently used in Japan), respectively, in units of genetic standard deviation. Survival rate increased the relative economic importance of later lactation traits and the first five lactation milk yields during the first 120 months from the start of the breeding scheme. In contrast, reliabilities of the estimated breeding value (EBV) in later lactation traits are lower than those of earlier lactation traits. We then sought to clarify the effects of applying single nucleotide polymorphism (SNP) on net merit to improve the reliability of EBV of later lactation traits to maximize their increased economic importance due to increase in survival rate. Net merit, selection accuracy, and HL increased by adding lactation persistency to the selection index whose component traits were only milk yields. Lactation persistency of the second and (especially) third parities contributed to increasing HL while maintaining the first five lactation milk yields compared with the selection index whose only component traits were milk yields. A selection index comprising the first three lactation milk yields and persistency accounted for 99.4% of net merit derived from a selection index whose components were identical to those for net merit. We consider that the selection index comprising the first three lactation milk yields and persistency is a practical method for increasing lifetime milk yield in the absence of data regarding HL. Applying SNP to the second- and third-lactation traits and HL increased net merit and HL by maximizing the increased economic importance of later lactation traits, reducing the effect of first-lactation milk yield on HL (genetic correlation (r_G) = -0.006), and by augmenting the effects of the second- and third-lactation milk yields on HL (r_G = 0.118 and 0.257, respectively). (**Key Words:** Economic Weights, Milk Yield, Persistency, Herd Life, Selection Index)

INTRODUCTION

High milk production and long herd life (HL) are important to the dairy industry. In Japan, the average number of lactations of a commercial dairy cow is about 3. Lifetime milk yield, in principle, is defined as a total milk yield until the time the cow is culled but can be defined as a total milk yield from as many as five lactations. Previous selection index coefficients of the first three lactation milk yields to maximize the first five lactation milk yields (Weller et al., 1984) ignored the differences in reliability of estimated breeding value (EBV) on various traits of the first three lactations. However, selection index coefficients can be affected by the reliability with which EBV predicts a particular component trait (Togashi et al., 2011). The reliability of EBV differs with selection traits of the first three lactation milk yields and lactation persistency as well as between bulls and dams selected as breeding candidates (Hagiya et al., 2010). Genetic superiority of animals selected as breeding candidates or genetic difference between selected and all the animals is estimated more precisely by allowing for differences in the reliabilities of index component traits.

Prolonging the HL of high-producing cows decreases replacement and health costs and thus increases profit. Herd life is a complex trait that is determined by survival rate, which in turn is influenced strongly by multiple factors such

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as milk production, disease, conformation, selection intensity, market conditions, and so forth. Obviously, improving the survival rate would increase HL. Multi-trait selection of breeding candidates in which HL is included as one of the component traits requires knowing the economic weight of HL in relation to that of all other component traits. Estimating the relative economic weight of HL requires milk, carcass, and calf revenues and feed, health, labor, and opportunity costs (Van Arendonk, 1991; Van Raden and Wiggans, 1995; Weigel et al., 1995; Jagannatha et al., 1998). Currently, the Japanese scheme of selection for lifetime performance is based on a linear combination of lifetime milk yield and durability (an indicator of HL), in which these traits are weighted by 1 and 0.389, respectively (NLBC and LIAJ, 2010).

Therefore, net merit is defined as a linear combination of total milk yield from the first five lactations and HL, weighted by 1 and 0.389, respectively, in units of genetic standard deviation. Thus, comparison of selection index is investigated based on the magnitude of net merit.

Improving lactation persistency improves animals' utilization of cheap roughage (Solkner and Fuchs, 1987), reduces stress due to high peak yield (Zimmermann and Sommer, 1973; Jakobsen, 2000; Yamazaki et al., 2010), increases profit (Dekkers et al., 1998), and prolongs HL (Weller et al., 2006). We therefore evaluated the effects of lactation persistency and milk yield during the first three lactations as component traits of the selection index on net merit.

Discounted rate is the quantification of the response to selection according to the discounted cash-flow procedure (Hill, 1971). In the current study, we investigated the effects of discounted and survival rates on net merit. We hypothesized that survival rate would increase relative to the economic importance of later compared with earlier lactation traits and would increase the accumulated economic value of the first five lactation milk yields during a given period. However, the reliability of EBV is lower for later compared with earlier lactation traits (Hagiya et al., 2010), making it essential to increase the reliability of EBV for later lactation traits to make good use of increased economic importance in later lactation traits due to increase in survival rate. Single-nucleotide polymorphism (SNP) has been applied to increase the reliability of EBV in young bulls (Van Raden et al., 2009), and the genetic correlation between HL and first-, second-, and third-lactation milk yield is -0.006, 0.118, and 0.257, respectively (Hagiya et al., 2010). We therefore assessed whether application of SNP to improve the reliabilities of EBVs for HL, lactation persistency and milk yield in later lactations consequently increased net merit and HL, reduced the effect of first-lactation milk yield on HL, and augmented the effects of second- and third-lactation milk yields on HL.

MATERIALS AND METHODS

Derivation of survival matrix

We divided the life cycle of a dairy cow into 5 stages: stage 1 refers to the period from birth to the end of the first lactation; stage 2 is from the end of the first lactation to the end of the second lactation; and so forth. The survival matrix $S_{i,j}$ then is derived, in which the row (i) represents the lactation number and the column (j) represents the age (in months) at the end of the ith lactation. Thus, matrix S represents the age distribution of a cow population. Currently in Japan, the average age at first calving is 25 months, and the calving interval is 14 months (MAFF, 2011). Let r_{01} be the survival rate from birth to the end of first lactation or the end of stage 1. Let r_{ij} be the survival rate from the end of the ith lactation or the end of the ith stage to the end of the jth lactation or the end of the jth stage, e.g., r_{12} = survival rate from the end of the first lactation or the end of the first stage to the end of the second lactation or the end of the second stage. The survival rate (r_{ij}) is determined by a cow being alive and getting pregnant from the end of the ith lactation to the end of the jth lactation. The survival rates of r_{01}, r_{12}, r_{23}, r_{34}, and r_{45} currently in Japan are 0.6900, 0.7773, 0.7525, 0.5936, and 0.5464, respectively (Hagiya et al., 2010). The survival matrix starts when a female calf is born. The investment period is set at 120 months. The elements of $S_{i\ j\ (i\ =\ 1,\ 2,\ 3,\ 4,\ 5\ stage;\ j\ =\ 1,2,\ ...,\ 120\ months)}$ are derived as described by Weller et al. (1984). Increased survival rates are set as t times as large as the current survival rate (t = 1.05, 1.1, 1.15, 1.2, and no loss rate of 100%).

The relative economic weights of the first five lactation milk yields

Genetic lifetime milk yield (H_5) is defined as follows:

$$H_5 = w_1G_1 + w_2G_2 + w_3G_3 + w_4G_4 + w_5G_5,$$

where G_i and w_i are the genetic value and relative economic weight of the ith lactation milk yield, respectively (i = 1 to 5). H_5 is genetic lifetime milk yield derived by using only milk yield for the first five lactations.

The discounted expressions (Hill, 1971; Weller et al., 1994) are as follows:

$$d_j = \frac{1}{(1+\delta)^j}$$

where d_j is the appropriate discounting factor, for which the subscript j is the time interval (in months) from the original

investment to mean trait expression ($j = 1, \ldots, 120$ months), and δ is the discounted rate per month %, e.g., δ = 0/12%, 1/12%, or 4/12% per month. The relative economic weights for the first five lactation milk yields ($\mathbf{w}'_5 = (w_1, w_2, w_3, w_4, w_5)$) reflect the actual average of each lactation milk yield, so that $\mathbf{w}_5$ is $\mathbf{w}_5 = \mathbf{AM}_{5\times5}\mathbf{S}_{5\times120}\mathbf{d}$ with the vector $\mathbf{d} = (d_1, \ldots d_{120})'$ and the diagonal matrix $\mathbf{AM}_{5\times5}$ whose diagonal elements are the averages of the ith lactation milk ($\overline{M}_i$, $i =$ 1 to 5). The discounted total milk yield during the given period of 120 months from the original investment is described as $\mathbf{w}'_5 \mathbf{1}$.

Net merit defined in terms of the first five lactation milk yields and HL

The relative economic weights (in genetic standard deviations) of total milk yield (the sum of the first five lactation milk yields) and HL were studied as: $w^*_{milk} : w^*_{HL} = 1 : 0.389$, where w^*_{milk} and w^*_{HL} are the relative economic weights (in genetic standard deviations) for the first five lactation milk yields and HL, respectively. The ratio of $w^*_{milk} : w^*_{HL} = 1 : 0.389$ is equivalent to the ratio of 7.2:2.8 currently used in Japan and is in close agreement with the reported value of 7.0:2.5 (Burnside et al., 1984; Allaire and Gibson, 1992; Weller and Ron, 1992; Dekkers, 1994). Net merit ($H^*_{net\ merit}$), defined in terms of the first five lactation milk yields and HL in genetic standard deviations, is as follows:

$$
\begin{aligned}
H^*_{net\ merit} \\
= \frac{\sigma_{H5}(w^a_1 G_1 + w^a_2 G_2 + w^a_3 G_3 + w^a_4 G_4 + w^a_5 G_5)}{\sigma_{H5}} \\
+ \frac{\sigma_{G_{HL}} w^a_6 G_{HL}}{\sigma_{G_{HL}}}
\end{aligned}
$$

where w^a_i (i = 1 to 5) is the relative economic weight for the ith lactation milk yield described as $w^a_i = w_i / (\sum_{i=1}^{5} w_i)$;

$\sum_{i=1}^{5} w^a_i = 1$, w^a_6 is the relative economic weight for HL,

$$\sigma_{H5} = (\text{Variance}(w^a_1 G_1 + w^a_2 G_2 + w^a_3 G_3 + w^a_4 G_4 + w^a_5 G_5))^{0.5}$$

and $\sigma_{G_{HL}}$ is the genetic standard deviation of HL. On the other hand, $w^*_{HL} / w^*_{milk} = \frac{2.8}{7.2} = \frac{w^a_6 \sigma_{G_{HL}}}{\sigma_{H5}}$, so that net merit

($H_{net\ merit}$) in units of actual values of milk (kg) and HL (days) is as follows:

$$
\begin{aligned}
H_{net\ merit} &= w^a_1 G_1 + w^a_2 G_2 + w^a_3 G_3 + w^a_4 G_4 + w^a_5 G_5 \\
&+ \frac{w^*_{HL}}{w^*_{milk}} \frac{\sigma_{H5}}{\sigma_{G_{HL}}} G_{HL} \\
&= w^a_1 G_1 + w^a_2 G_2 + w^a_3 G_3 + w^a_4 G_4 + w^a_5 G_5 + w^a_6 G_{HL}
\end{aligned}
$$

Comparison of selection indices in terms of maximizing net merit

Lactation milk yield and persistency during the first one, two, or three parities are taken as the component traits of selection indices (I_1-I_6) to maximize net merit ($H_{net\ merit}$) and to clarify the effects of adding lactation persistency as a component trait of selection index to selection index consisting of only milk yields. Selection index (I_7), comprising the same components as those for net merit, is set as a basis of comparison:

$$I_1 = M_1,$$

$$I_2 = b_1 M_1 + b_2 P_1,$$

$$I_3 = b_1 M_1 + b_2 M_2,$$

$$I_4 = b_1 M_1 + b_2 M_2 + b_3 P_1 + b_4 P_2,$$

$$I_5 = b_1 M_1 + b_2 M_2 + b_3 M_3,$$

$$I_6 = b_1 M_1 + b_2 M_2 + b_3 M_3 + b_4 P_1 + b_5 P_2 + b_6 P_3, \text{ and}$$

$$I_7 = b_1 M_1 + b_2 M_2 + b_3 M_3 + b_4 M_4 + b_5 M_5 + b_6 hl,$$

where M_i, P_i, and hl are the EBV for the ith lactation milk yield, i^{th} lactation persistency, and HL, respectively and b_i is the selection index coefficient for the ith component trait of selection index. Lactation persistency is defined as the difference in EBVs for 240 DIM and 60 DIM (Togashi et al., 2008). The selection index is derived as described by Togashi et al. (2011), in which differences between the reliabilities of the EBV of the component traits of the selection index are taken into consideration.

Here we use the index $I_6 = b_1 M_1 + b_2 M_2 + b_3 M_3 + b_4 P_1 + b_5 P_2 + b_6 P_3$ as an example to demonstrate the derivation. In matrix notation, the index can be written as,

$$I_6 = \mathbf{b}'_6 \mathbf{g}_6,$$

where $b_6^{'} = (b_1\ b_2\ b_3\ b_4\ b_5\ b_6)$ and $g_6^{'} = (M_1\ M_2\ M_3\ P_1\ P_2\ P_3)$.

As indicated earlier, the goal is to maximize the genetic superiority of animals selected as breeding candidates in terms of net merit ($H_{net\ merit}$). The covariance matrix between I_6 and $H_{net\ merit}$ is as follows:

$$\sigma_{I_6, H_{net\ merit}} = b_6^{'} C_6 w ,$$

where $\mathbf{w'} = (w_1^a\ w_2^a\ w_3^a\ w_4^a\ w_5^a\ w_6^a)$ and

$$\mathbf{C_6} = \begin{bmatrix} r_{G1}^2\sigma_{G1}^2 & r_{G1}r_{G2}\sigma_{G1,2} & r_{G1}r_{G3}\sigma_{G1,3} & r_{G1}r_{G4}\sigma_{G1,4} & r_{G1}r_{G5}\sigma_{G1,5} & r_{G1}r_{GHL}\sigma_{G1,GHL} \\ r_{G2}r_{G1}\sigma_{G2,1} & r_{G2}^2\sigma_{G2}^2 & r_{G2}r_{G3}\sigma_{G2,3} & r_{G2}r_{G4}\sigma_{G2,4} & r_{G2}r_{G5}\sigma_{G2,GHL} & r_{G2}r_{GHL}\sigma_{G2,GHL} \\ r_{G3}r_{G1}\sigma_{G3,1} & r_{G3}r_{G2}\sigma_{G3,2} & r_{G3}^2 & r_{G3}r_{G4}\sigma_{G3,4} & r_{G3}r_{G5}\sigma_{G3,5} & r_{G3}r_{GHL}\sigma_{G3,GHL} \\ r_{GP1}r_{G1}\sigma_{GP1,G1} & r_{GP1}r_{G2}\sigma_{GP1,G2} & r_{GP1}r_{G3}\sigma_{GP1,G3} & r_{GP1}r_{G4}\sigma_{GP1,G4} & r_{GP1}r_{G5}\sigma_{Gp1,G5} & r_{GP1}r_{GHL}\sigma_{GP1,GHL} \\ r_{GP2}r_{G1}\sigma_{GP2,G1} & r_{GP2}r_{G2}\sigma_{GP2,G2} & r_{GP2}r_{G3}\sigma_{GP2,G3} & r_{GP2}r_{G4}\sigma_{GP2,G4} & r_{GP2}r_{G5}\sigma_{GP2,G5} & r_{GP2}r_{GHL}\sigma_{GP2,GHL} \\ r_{GP3}r_{G1}\sigma_{GP3,G1} & r_{GP3}r_{G2}\sigma_{GP3,G2} & r_{GP3}r_{G3}\sigma_{GP3,G3} & r_{GP3}r_{G4}\sigma_{GP3,G4} & r_{GP3}r_{G5}\sigma_{GP3,G5} & r_{GP3}r_{GHL}\sigma_{GP3,GHL} \end{bmatrix}$$

The variance of I_6 is as follows:

$$\sigma_{I_6}^2 = b_6' P_6 b_6 ,$$

$$\mathbf{P_6} = \begin{bmatrix} r_{G_1}^2\sigma_{G_1}^2 & r_{G_1}r_{G_2}\sigma_{G_{1,2}} & r_{G_1}r_{G_3}\sigma_{G_{1,3}} & r_{G_1}r_{GP1}\sigma_{G_1,GP1} & r_{G_1}r_{GP2}\sigma_{G_1,GP2} & r_{G_1}r_{GP3}\sigma_{G_1,GP3} \\ r_{G_1}r_{G_2}\sigma_{G_{2,1}} & r_{G_2}^2\sigma_{G_2}^2 & r_{G_2}r_{G_3}\sigma_{G_{2,3}} & r_{G_2}r_{GP1}\sigma_{G_2,GP1} & r_{G_2}r_{GP2}\sigma_{G_2,GP2} & r_{G_2}r_{GP3}\sigma_{G_2,GP3} \\ r_{G_1}r_{G_3}\sigma_{G_{3,1}} & r_{G_2}r_{G_3}\sigma_{G_{3,2}} & r_{G_3}^2\sigma_{G_3}^2 & r_{G_3}r_{GP1}\sigma_{G_3,GP1} & r_{G_3}r_{GP2}\sigma_{G_3,GP2} & r_{G_3}r_{GP3}\sigma_{G_3,GP3} \\ r_{GP1}r_{G_1}\sigma_{GP1,G_1} & r_{GP1}r_{G_2}\sigma_{GP1,G_2} & r_{GP1}r_{G_3}\sigma_{GP1,G_3} & r_{GP1}^2\sigma_{GP1}^2 & r_{GP1}r_{GP2}\sigma_{GP1,GP2} & r_{GP1}r_{GP3}\sigma_{GP1,GP3} \\ r_{GP2}r_{G_1}\sigma_{GP2,G_1} & r_{GP2}r_{G_2}\sigma_{GP2,G_2} & r_{GP2}r_{G_3}\sigma_{GP2,G_3} & r_{GP2}r_{GP1}\sigma_{GP2,GP1} & r_{GP2}^2\sigma_{GP2}^2 & r_{GP2}r_{GP3}\sigma_{GP2,GP3} \\ r_{GP3}r_{G_1}\sigma_{GP3,G_1} & r_{GP3}r_{G_2}\sigma_{GP3,G_2} & r_{GP3}r_{G_3}\sigma_{GP3,G_3} & r_{GP3}r_{GP1}\sigma_{GP3,GP1} & r_{GP3}r_{GP2}\sigma_{GP3,GP2} & r_{GP3}^2\sigma_{GP3}^2 \end{bmatrix}$$

where GP_i is the genetic value of the ith lactation persistency, r_{G_i} is the accuracy of the ith lactation milk yield EBV, and r_{GPi} is the accuracy of the ith lactation persistency EBV. The reliabilities of the EBV of selection traits of candidate bulls and the genetic parameters were derived from Hagiya et al. (2010) and Togashi et al. (2008). The square of the accuracy is reliability. The average reliability is used in this study.

The genetic superiority of selected bulls as breeding candidates or the genetic difference between candidate bulls and all the bulls due to selection on I_6 for net merit ($H_{net\ merit}$) is as follows:

$$\Delta H_{net\ merit} = \sigma_{I_6} \cdot \bar{i} ,$$

where σ_{I_6} is the standard deviation of the index I_6 and $\bar{i}$ is the selection intensity.

And selection accuracy is as follows:

$$\sigma_{I_6} / \sigma_{H_{net\ merit}} = \sqrt{b_6' P_6 b_6} / \sqrt{w'Gw}$$

where G is the genetic covariance matrix of the first five

lactation milk yields and HL. The genetic superiorities of selected bulls as breeding candidates in the first five lactation milk yields ($\Delta G_1, \Delta G_2, ..., \Delta G_5$) and HL ($\Delta G_{HL}$) are shown as follows:

$$\begin{bmatrix} \Delta G_1 & \Delta G_2 & \Delta G_3 & \Delta G_4 & \Delta G_5 & \Delta G_{HL} \end{bmatrix}' = C_6' b_6\ \bar{i}/\sigma_{I_6} .$$

We compared the seven selection indices in terms of net merit, selection accuracy, genetic superiorities over the total of the first through fifth lactation milk yields ($\sum_{i=1}^{5}\Delta G_i$), and herd life (ΔHL). Selection intensity was set to unity ($\bar{i} = 1$) for all selection criteria compared in the current study.

Application of SNP

Currently in Japan, the reliabilities of EBV among selected bulls as breeding candidates for milk yield of the first five lactations are 0.816, 0.708, 0.597, 0.550, and 0.500, respectively; those for persistency of the first three lactations are 0.689, 0.612, and 0.493, respectively; and that for HL is 0.570 (Hagiya et al., 2010). The reliabilities of first-lactation traits are higher than those of second or third lactation traits, because collection of records is more rapid for first-lactation compared with second- and third-lactation traits. Using SNP to improve reliability is more important for second- or third-lactation traits than first-lactation traits, due to this difference in data collection time. Therefore, we considered three scenarios: increasing the reliabilities of second- and third-lactation traits and of HL by 10% while maintaining the reliabilities of first-lactation traits at their current levels; increasing the reliabilities of second- and third-lactation traits and of HL by 20% while maintaining the reliabilities of first-lactation traits at their current levels, and increasing the reliabilities of second- and third-lactation traits and of HL by 20% and the reliabilities of first-lactation traits by 10%.

RESULTS AND DISCUSSION

Effects of survival and discounted rates on the relative economic weights of the first five lactation milk yields

The relative economic weights for the first five lactation milk yields in terms of actual milk yield (kg) are shown in Table 1, which is based on survival matrix S_{ij} and shows the effects of both survival and discounted rates on the relative economic weights of the first five lactation milk yields, the pooled weights of the third, fourth, and fifth lactation milk yields, and these economic weights under a 100% survival rate. The relative economic weights of the second, third, fourth, and fifth lactation milk yields (w_2, w_3, w_4, and w_5) were expressed as ratios of the first lactation

Table 1. Relative economic weights of the first five lactation milk yields

Discounted rate %/month)	i^{th} lactation milk ($\overline{M}_i$ kg)[1]	Level of survival rate (t times as large as the current survival rate)					
		1.0	1.05	1.1	1.15	1.2	Survival rate[2]
0/12	1	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	0.8747	0.9184	0.9622	1.0059	1.0496	1.1253
	3	0.6842	0.7543	0.8278	0.9048	0.9852	1.1697
	4	0.3803	0.4403	0.5062	0.5784	0.6572	1.0953
	5	0.2036	0.2475	0.2981	0.3561	0.4221	1.0731
	3,4,5	1.2681	1.4420	1.6321	1.8392	2.0645	3.3381
	Total milk[3]	1.0000	1.1227	1.2580	1.4070	1.5709	2.5194
1/12	1	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	0.8661	0.9094	0.9527	0.9960	1.0393	1.1142
	3	0.6696	0.7382	0.8102	0.8855	0.9642	1.1447
	4	0.3691	0.4273	0.4913	0.5614	0.6378	1.0631
	5	0.1953	0.2374	0.2859	0.3416	0.4050	1.0294
	3,4,5	1.2340	1.4029	1.5874	1.7884	2.0070	3.2372
	Total milk[3]	1.0000	1.1219	1.2561	1.4039	1.5663	2.5018
4/12	1	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	0.8403	0.8823	0.9243	0.9664	1.0084	1.0811
	3	0.6274	0.6917	0.7591	0.8297	0.9034	1.0726
	4	0.3371	0.3903	0.4487	0.5128	0.5826	0.9710
	5	0.1723	0.2094	0.2522	0.3013	0.3572	0.9079
	3,4,5	1.1367	1.2913	1.4600	1.6437	1.8432	2.9515
	Total milk[3]	1.0000	1.1193	1.2505	1.3945	1.5525	2.4499

[1] $\overline{M}_1 = 7756.9$ $\overline{M}_2 = 9013.9$ $\overline{M}_3 = 9369.4$ $\overline{M}_4 = 9387.4$ $\overline{M}_5 = 9196.4$. [2] Survival rate = 100%.

[3] Total milk = Total discounted milk yield for the first five lactations during 120 months in compared with that of the current survival rate.

milk (w_1) by setting $w_1 = 1$. The relative economic weights of w_2 through w_5 increased as the survival rate increased from t = 1 to t = 1.2 for all discounted rates. For a given survival rate, the economic weights of w_2 through w_5 decreased as the discounted rate increased because the time to reach the second through fifth lactations is longer than to reach the first lactation.

Among the 9 combinations determined at all levels of discounted rates (0/12%, 1/12%, and 4/12% per month) and survival rates (t = 1.0, 1.05, and1.1; t times as large as the current survival rate), the relative economic weight of the first lactation was greater than that of the second lactation, which in turn was greater than that of third lactation and so forth ($w_1 > w_2 > w_3 > w_4 > w_5$). This effect occurred because survival rate decreases as parity increases, as mentioned earlier, i.e., the survival rates of r_{01}, r_{12}, r_{23}, r_{34}, and r_{45} are 0.6900, 0.7773, 0.7525, 0.5936, and 0.5464, respectively (Hagiya et al., 2010). The decrease in economic weight from the third to fifth parity was greater than that from the first to third parity because survival rate decreased more from the third to fifth parity than from the first to third parity. The economic weight of the fourth and fifth lactation milk yields increased with the survival rate.

The relative economic weight of the pooled third, fourth,

and fifth lactation milk yields was higher than that of first or second lactation milk yield, especially at low discounted rates and high survival rates. This result indicates that, compared with first- or second-lactation milk yield, the third-, fourth-, and fifth-lactation milk yields play important roles in the genetic improvement of lifetime performance, especially under low discounted and high survival rates. As an example, when the survival rate improved by 20% (t = 1.2) under a discounted rate of 0, the relative economic weight of the pooled third-, fourth-, and fifth-lactation milk yields was about two times greater than that of the first parity.

Currently in Japan, the first three lactation milk yields are given equal economic weights. This assignment overestimates the relative economic weight of the second and third lactations (w_2 and w_3), particularly under the current survival rate (t = 1). Overestimation of w_2 and w_3 decreased as the survival rate increased. In contrast, when the survival rate was achieved without loss (100%), the relative economic weight of the third lactation was greater than that of the second lactation, which in turn was greater than that of first lactation ($w_3 > w_2 > w_1$) under discounted rates of 0/12% and 1/12% per month. This result occurs because the average yield of the third lactation milk is

greater than that of the second lactation milk, which in turn is greater than that of first lactation milk ($\overline{M}_3 > \overline{M}_2 > \overline{M}_1$).

The value of $\mathbf{w}_5'1$ (the total discounted yields of the first through fifth lactation milks) during the 120 months from the original investment is shown in Table 1 as a ratio of the total discounted yields of the first through fifth lactation milks under the current survival rate. The total discounted yields of the first through fifth lactation milks during 120 months increased with increasing survival rate. For example, under a discounted rate of 0, when survival rate improved by 20% (t = 1.2), the total discounted yields of the first through fifth lactation milks increased by 1.57 times compared with that under the current survival rate (t = 1). Therefore, it is important to improve survival rate through both genetics and management.

Comparison of selection indices in terms of maximizing net merit

The selection accuracy and genetic superiorities of net merit, the total yield of the first through fifth lactation milks and HL derived by using selection indices (I_1 to I_7) for selected bulls as breeding candidates under the current survival rate and a discounted rate of 0 are shown in Table 2. Net merit and selection accuracy increased by adding lactation persistency as a component trait to selection index comprising only milk yields. That is, net merit and selection accuracy during the first; first and second; and first, second, and third parity components was larger in I_2 ($b_1M_1+b_2P_1$) than in I_1 (M_1), in I_4 ($b_1M_1+b_2M_2+b_3P_1+b_4P_2$) than in I_3 ($b_1M_1+b_2M_2$), and in I_6 ($b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_3$) than in I_5 ($b_1M_1+b_2M_2+b_2M_3$), respectively. In addition, the genetic superiority of HL in first and second parity and in first, second, and third parity components was larger in I_4 ($b_1M_1+b_2M_2+b_3P_1+b_4P_2$) than in I_3 ($b_1M_1+b_2M_2$) and in I_6 ($b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_3$) than in I_5 ($b_1M_1+b_2M_2+b_2M_3$), respectively. In particular, the genetic superiority of HL was 45.4 days from I_6 compared with 39.0 days from I_5. The genetic superiority of the total yield of the first through fifth lactation milks in the first and second and first, second, and third parity components were equivalent between I_3 ($b_1M_1+b_2M_2$) and I_4 ($b_1M_1+b_2M_2+$

$b_3P_1+b_4P_2$) and between I_5 ($b_1M_1+b_2M_2+b_2M_3$) and I_6 ($b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_3$), respectively. Therefore lactation persistency during the second and (especially) third parity contributed to increasing net merit, in which HL was increased while the first five lactation milk yields were maintained at the same levels derived from the selection index consisting of only milk yields.

The genetic superiority of the first five lactation milk yields was highest for I_2 ($b_1M_1+b_2P_1$) among the six indices (I_1 to I_6), and followed by I_1 (M_1). These results reflect the high genetic correlations between the first-lactation milk yield and second- through fifth-lactation milk yields ($r_G = 0.759$ to 0.974), the moderate genetic correlation between lactation persistency during the first parity with the first five lactation milk yields ($r_G = 0.42$ to 0.53), and that the reliabilities of the EBVs for milk yield and lactation persistency rank (in descending order) as M_1, M_2, M_3 and P_1, P_2, P_3, respectively.

The order of genetic superiority of HL was I_6 ($b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_6$)>$I_5$ ($b_1M_1+b_2M_2+b_2M_3$) >I_4 ($b_1M_1+b_2M_2+b_3P_1+b_4P_4$)>$I_3$ ($b_1M_1+b_2M_2$)>I_1 (M_1) $\cong$ I_2 ($b_1M_1+b_2P_1$). I_1 and I_2 yielded the smallest ΔH_{HL}, due to the low genetic correlations between HL and first-lactation milk yield (-0.006) and persistency (0.09). Tsuruta et al. (2004) found that the genetic correlation between productive life and milk yield declined from positive to 0 over the years from 1979 to 1993, mainly in response to changes in producers' culling practices.

Dairy producers' decisions regarding culling cows reflect various factors such as milk yield, reproduction problems, mastitis, lameness, and labor costs. All of these factors can change over time. Functional traits (such as resistance to mastitis and lameness, fertility, calving ease, and longevity) are defined as the characteristics of an animal that increase production efficiency through reduced input costs rather than increased output of products (Groen et al., 1998). High milk production during the first lactation decreases the efficacy of the immune system in the udder and leads to damage that persists throughout subsequent lactations (Rupp et al., 2000). The genetic superiority of HL due to index I_5 ($b_1M_1+b_2M_2+b_3M_3$) or I_6 ($b_1M_1+b_2M_2+$

Table 2. Genetic superiorities of selected bulls as breeding candidates based on selection indices compared (I_1 to I_7)[1] under the current survival and zero discounted rates

	I_1	I_2	I_3	I_4	I_5	I_6	I_7
Net merit[2]	594.1	597.8	617.1	619.1	657.0	663.5	667.5
Selection accuracy	0.722	0.726	0.750	0.753	0.799	0.806	0.811
1 to 5 parity milk (kg)	2,743.9	2,753.4	2,698.6	2,695.1	2,717.9	2,717.9	2,722.6
Herd life(days)	-0.6	0.6	14.8	16.4	39.0	45.4	46.6

[1] $I_1 = M_1$, $I_2 = b_1M_1+b_2P_1$, $I_3 = b_1M_1+b_2M_2$, $I_4 = b_1M_1+b_2M_2+b_3P_1+b_4P_2$, $I_5 = b_1M_1+b_2M_2+b_3M_3$, $I6 = b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_3$, and $I_7 = b_1M_1+b_2M_2+b_3M_3+b_4M_4+b_5M_5+b_6h_1$, where Mi and Pi is i[th] lactation milk yield and persistency EBV, respectively, and hl and b_i is EBV for herd life and selection index coefficient for i[th] component trait, respectively.
[2] Net merit is a linear combination of the first five-lactation milk yields and herd life weighted by 1 and 0.389 in unit of genetic standard deviation.

$b_3M_3+b_4P_1+b_5P_2+b_6P_3$) was about 2.5 times greater than that due to I_4 ($b_1M_1+b_2M_2+b_3P_1+b_4P_2$). These results indicate that milk yield during and persistency of the third lactation play important roles in determining the duration of HL, because third-lactation milk yield has a higher genetic correlation with HL ($r_G = 0.257$) than does either the first- ($r_G = -0.006$) or second- ($r_G = 0.118$) lactation milk yields, and third-lactation persistency has a higher genetic correlation with HL ($r_G = 0.210$) than does either the first- ($r_G = 0.090$) or second- ($r_G = 0.180$) lactation persistency. The milk yield or persistency of the lactation closest to the culling stage of a cow is much more important than that far back from the culling stage in extending the HL.

The component traits of selection index (I_7) are identical to those that define net merit components. This similarity means that net merit and selection accuracy due to selection index (I_7) are maximal in improving net merit ($H_{net\ merit}$).

Net merit due to I_6 ($b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_6$) was 99.4% of that of selection index (I_7). Net merit, selection accuracy, and HL based on I_6 were the largest among indices (I_1 to I_6). The first five lactation milk yields based on I_6 was the largest among indices (I_3 to I_6). The first five lactation milk yields based on I_1 or I_2 were larger than those based on I_3 through I_6. However, HL based on I_1 or I_2 was nearly 0. Furthermore, collecting data for HL is time-consuming and costly (Smith and Quaas, 1984). Therefore, selection index (I_6), which includes total milk yield and persistency of the first three lactations, as modified by the trait-specific EBVs, is a practical and favorable means of improving lifetime milk yield in the absence of data on HL.

Effects of survival and discounted rates on selection accuracy, HL, and first through fifth lactation milk yields

The effects of survival and discounted rates on selection accuracy, net merit, HL, and total milk yield during the first through fifth lactations according to selection index I_6 are shown in Table 3. As the discounted rate increased, net merit and selection accuracy increased but HL decreased because increased discounted rate puts greater relative economic weight on earlier rather than later lactations (Table 1) and because the reliabilities of the associated EBVs are higher for earlier rather than later lactation milk yields. Net merit and selection accuracy decreased slightly and HL increased when survival rate increased because increased survival rate puts greater economic weight on later compared with earlier lactations (Table 1).

Given the current survival rate (t = 1) and a discounted rate of 0% per month, the genetic superiority of selected bulls as breeding candidates in terms of total milk yield for the first through fifth lactations was 2,717.9 kg, according to I_6. Given the same survival rate (t = 1), when the discounted rate increased from 0% to 4/12% per month, the

Table 3. Net merit, selection accuracy, and genetic superiorities of selected bulls as breeding candidates for first through fifth lactation milk yields, and for herd life based on selection index $(I_6)^1$ at increased survival and discounted rates

	Discounted rate (%/month)	Survival rate[3]	I_6
Net merit[2]	0/12	1	663.5
	0/12	1.2	651.8
	4/12	1	665.9
	4/12	1.2	654.6
Selection accuracy	0/12	1	0.806
	0/12	1.2	0.790
	4/12	1	0.810
	4/12	1.2	0.794
A total of the 1st to 5th lactation milk yields (kg)	0/12	1	2,717.9
	0/12	1.2	2,699.3
	4/12	1	2,721.6
	4/12	1.2	2,704.0
Herd life (ΔHL, d)	0/12	1	45.4
	0/12	1.2	47.9
	4/12	1	44.9
	4/12	1.2	47.3

[1] $I_6 = b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_3$, where Mi and Pi are i[th] lactation milk yield and persistency EBV, respectively, and hl and b_i is EBV for herd life and selection index coefficient for i[th] component trait, respectively.

[2] Net merit is a linear combination of the first five-lactation milk yields and herd life weighted by 1 and 0.389 in unit of genetic standard deviation.

[3] t times as high as the current survival rate.

genetic superiority in terms of total milk yield for the first through fifth lactations increased to 2,721.6 kg, due to the increased reliabilities of the EBVs of the earlier lactation milk yields. Similarly, given the same discounted rate (0% per month), when the survival rate increased from t = 1.0 to t = 1.2, the genetic superiority in terms of total milk yield for the first through fifth lactations decreased from 2,717.9 to 2,699.3 kg, due to the decreased reliabilities of the EBVs and increased relative economic weights of later lactations.

Under the current survival rate (t = 1) and a discounted rate of 0%, genetic superiority in terms of HL was 45.4 days, according to I_6. Under the same survival rate (t = 1), when the discounted rate increased from 0% to 4/12% per month, genetic superiority in terms of HL due to I_6 decreased from 45.4 to 44.9 days (only approximately 1.0%). When the survival rate increased by 20% (t = 1.2) under the same discounted rate (0% per month), genetic superiority in terms of HL due to I_6 increased from 45.4 to 47.9 days (approximately 5%). This result indicates that increasing the discounted rate slightly shortens HL whereas increasing the survival rate greatly prolongs HL.

Applying SNP to maximize the economic weights of later lactation milk yields

The net merit, selection accuracy, and genetic superiorities associated for selected bulls as breeding candidates based on selection index (I_6) are shown in Table 4, for which SNP was applied to increase the reliabilities of the trait-specific EBVs. Net merit and selection accuracy decreased with increasing survival rate with or without input from SNP. In the first scenario we tested, the ratio of net merit at 20% increased survival rate to that of the current survival rate was 0.9823 to 0.9830 without applying SNP but 0.9863 to 0.986 with SNP. In particular, the net merit ratio based on the second scenario, in which the reliabilities of second- and third-lactation traits and HL were increased by 20% while those of first-lactation traits were maintained at the current levels, was relatively high, i.e., 0.9890 to 0.9897. Similarly, the ratio of selection accuracy at 20% increased survival rate to that of the current survival rate was 0.9801 to 0.9802 without SNP but 0.9833 to 0.9845 with SNP, with that of the ratio based on the second scenario being particularly high, i.e., 0.9861 to 0.9873. Therefore, using SNP reduced the decreases in net merit and selection accuracy that otherwise were accompanied by the decrease in reliabilities of later lactation traits. In all three scenarios we tested, application of SNP regarding later lactation traits and HL increased net merit and selection accuracy. This trend becomes more evident as the difference in reliability between second- and third-lactation traits and first lactation traits becomes larger (as in the second scenario we tested).

In all alternative scenarios tested, applying SNP increased the first five lactation milk yields compared with these traits in the current scenario without SNP, and this increase became more pronounced as reliability increased (third scenario). Similarly, adding SNP data increased HL in all the scenarios (particularly the second) compared with that of the current scenario without SNP. The longer HL that occurred during the second scenario compared with that which occurred during the third scenario, where the reliabilities of second- and third-lactation traits and HL were increased by 20% while those of first-lactation traits were increased by 10%, reflects the genetic correlation between HL and the first-, second-, and third-lactation milk yields (-0.006, 0.118, and 0.257, respectively). Therefore, applying SNP to increase the reliabilities of EBV of second- and third-lactation traits and HL while maintaining those of

Table 4. Net merit, selection accuracy, and genetic superiorities of selected bulls as breeding candidates for first through fifth lactation milk yields, and for herd life based on selection index (I_6)[1] at increased survival and discount rates when reliability of EBV is increased by SNP[2]

	Discounted rate (%/month)	Survival rate[3]	I_6 (without SNP)	1.1 or 1.2 times reliability by SNP		
				1 to 1.1[4]	1 to 1.2[4]	1.1 to 1.2[4]
Net merit[5]	0/12	1	663.5	687.8	710.0	719.2
	0/12	1.2	651.8	678.4	702.2	709.2
	0/12	Ratio of 1.2/1	0.9823	0.9863	0.9890	0.9861
	4/12	1	665.9	689.7	711.4	721.2
	4/12	1.2	654.6	680.6	704.1	711.6
	4/12	Ratio of 1.2/1	0.9830	0.9868	0.9897	0.9867
Selection accuracy	0/12	1	0.806	0.836	0.863	0.874
	0/12	1.2	0.790	0.822	0.851	0.860
	0/12	Ratio of 1.2/1	0.9801	0.9833	0.9861	0.9840
	4/12	1	0.810	0.839	0.865	0.877
	4/12	1.2	0.794	0.826	0.854	0.863
	4/12	Ratio of 1.2/1	0.9802	0.9845	0.9873	0.9840
A total of the 1st to 5th lactation milks (kg)	0/12	1	2,717.9	2,830.5	2,925.3	2,959.4
	0/12	1.2	2,699.3	2,812.0	2,906.8	2,940.0
	4/12	1	2,721.6	2,834.2	2,929.0	2,963.3
	4/12	1.2	2,704.0	2,816.6	2,911.4	2,944.9
Herd life (ΔHL,d)	0/12	1	45.4	48.3	51.0	50.3
	0/12	1.2	47.9	50.7	53.5	52.9
	4/12	1	44.9	47.7	50.5	49.8
	4/12	1.2	47.3	50.1	52.9	52.3

[1] $I_6 = b_1M_1+b_2M_2+b_3M_3+b_4P_1+b_5P_2+b_6P_3$ where M_i and P_i are i^{th} lactation milk yield and persistency EBV, respectively, and hl and b_i is EBV for herd life and selection index coefficient for i^{th} component trait, respectively.

[2] SNP = Single nucleotide polymorphism. [3] t times as high as the current survival rate.

[4] Reliability increase as t times greater than the current reliability of estimated breeding value for the 1st, 2nd and 3rd lactation traits, respectively.

[5] Net merit is a linear combination of the first five-lactation milk yields and herd life weighted by 1 and 0.389 in unit of genetic standard deviation.

first-lactation traits at their current levels increased net merit and HL by maximizing the increased economic importance of later lactation traits resulting from increased survival rates, by reducing the effect of first-lactation milk yield on HL, and by augmenting the effects of the second- and third-lactation milk yields on HL.

CONCLUSION

Net merit, selection accuracy, and HL increased by adding lactation persistency to the selection index whose omponent traits were only milk yields. Lactation persistency of the second and (especially) third parities contributed to increasing HL while maintaining the first five lactation milk yields compared with the selection index whose only component traits were milk yields. A selection index comprising the first three lactation milk yields and persistency accounted for 99.4% of the net merit derived from a selection index whose components were identical to those for net merit. We consider this selection index to be a practical means to increase lifetime milk yield in the absence of data on HL.

Increasing survival rate increased the first five lactation milk yields during the 120 months from the start of the breeding scheme. In particular, increasing survival rate by 20% increased the total discounted milk yields of the first through fifth lactations during the 120 months by 1.57 times compared with the total discounted milk yields at the current survival rate. It is important to improve survival rate through both genetics and management.

Survival rate increased the relative economic importance of later lactation traits. However, the reliabilities of later lactation traits are lower than those of earlier lactation traits, and applying SNP to improve the reliabilities of the EBVs of later lactation traits and HL made the most of the increased relative economic importance of later lactation traits that resulted from increases in survival rate. Overall, using SNP to increase the reliabilities of EBVs of second- and third-lactation traits while keeping those of first-lactation traits at their current levels increased net merit and HL by making the most of the increased economic importance of later lactation traits subsequent to increase in survival rate, by reducing the effect of first-lactation milk yield on HL ($r_G = -0.006$), and by augmenting the effects of second- and third-lactation milk yields on HL ($r_G = 0.118$ and 0.257, respectively).

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