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Effects of selection index coefficients that ignore reliability on economic weights and selection responses during practical selection

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Objective: In practical breeding, selection is often performed by ignoring the accuracy of evaluations and applying economic weights directly to the selection index coefficients of genetically standardized traits. The denominator of the standardized component trait of estimated genetic evaluations in practical selection varies with its reliability. Whereas theoretical methods for calculating the selection index coefficients of genetically standardized traits account for this variation, practical selection ignores reliability and assumes that it is equal to unity for each trait. The purpose of this study was to clarify the effects of ignoring the accuracy of the standardized component trait in selection criteria on selection responses and economic weights in retrospect.
Methods: Theoretical methods were presented accounting for reliability of estimated genetic evaluations for the selection index composed of genetically standardized traits.
Results: Selection responses and economic weights in retrospect resulting from practical selection were greater than those resulting from theoretical selection accounting for reliability when the accuracy of the estimated breeding value (EBV) or genomically enhanced breeding value (GEBV) was lower than those of the other traits in the index, but the opposite occurred when the accuracy of the EBV or GEBV was greater than those of the other traits. This trend was more conspicuous for traits with low economic weights than for those with high weights.
Conclusion: Failure of the practical index to account for reliability yielded economic weights in retrospect that differed from those obtained with the theoretical index. Our results indicated that practical indices that ignore reliability delay genetic improvement. Therefore, selection practices need to account for reliability, especially when the reliabilities of the traits included in the index vary widely.

Keywords: Economic Weight; Selection Index; Selection Responses; Quantitative Genetics; Cattle

INTRODUCTION

In practical selection [1,2], the economic value of each trait is often used directly as the coefficient of the standardized component trait, which is expressed as the ratio of estimated breeding value (EBV) or genomically enhanced breeding value (GEBV) to its standard deviation. Alternatively, the aggregate genotype or breeding goal is defined as a linear combination of true genetic values, each weighted by its relative economic value. Selection index coefficients are derived on the basis of selection index theory [3]. Accuracy of selection refers to the correlation between true and the estimated breeding values (EBV or GEBV) for selection candidates with the same amount of information in individual trait [4-6]. Reliability, which is the square of accuracy, is the proportion of true genetic variance explained by the EBVs or GEBVs. Reliability is recalculated every time EBV or GEBV is computed. That is, reliability changes every selection as a consequence of calculating EBV or GEBV. As a result, the denominator of the standardized component trait of estimated genetic evaluations (EBV or GEBV) in practical selection varies with the reliability. Therefore, although the coefficient of the standardized component trait used to accomplish a breeding goal should be adjusted to account for the varying size of the denominator or reliability, this adjustment is not made during practical selection and remains the same throughout all calculations or every selection. In other words, practical selection ignores the true reliability or uncertainty of estimated breeding evaluations and assumes that reliability is equal to unity for each trait.

Some livestock producers develop selection index weights to maximize the change in the dollar value of the animals in a herd on the basis of the producer's goals. In such practical dairy-farm breeding practices, the need to adjust reliability according to the EBV or GEBV of a trait is liable to be ignored when these custom made indices are developed. Our aim here was to clarify the effects of ignoring the accuracy of the standardized component trait in selection criteria on selection responses and economic weights in retrospect.

MATERIALS AND METHODS

The practical index and theoretical indices

The practical index (I_p), theoretically correct indices (I_{c1} and I_{c2}) corresponding to the practical index, and net merit (H) were defined as follows:

$$I_p = \sum_{i=1}^{m} a_i \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} = \mathbf{a}' \hat{\mathbf{g}}_{\sigma_{\hat{g}}},$$

$$I_{c1} = \sum_{i=1}^{m} b_{\sigma_{\hat{g}_i}} \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} = \mathbf{b}'_{\sigma_{\hat{g}}} \hat{\mathbf{g}}_{\sigma_{\hat{g}}},$$

$$I_{c2} = \sum_{i=1}^{m} b_{\sigma_{g_i}} \frac{\hat{g}_i}{\sigma_{g_i}} = \mathbf{b}'_{\sigma_g} \hat{\mathbf{g}}_{\sigma_g},$$

and

$$H = \sum_{i=1}^{m} a_i \frac{g_i}{\sigma_{g_i}} = \mathbf{a}' \mathbf{g}_{\sigma_g},$$

Where,

a_i = a known economic value for the ith trait (i = 1 , , , , m),

a = a vector of m known economic values,

$\hat{g}_i$ = a known EBV or GEBV for the ith trait (i = 1 , , , , m),

$\frac{\hat{g}_i}{\sigma_{\hat{g}_i}}$ = a known EBV or GEBV divided by its standard deviation in the whole population ($\sigma_{\hat{g}_i}$) for the ith trait (i = 1 , , , , m),

$\hat{\mathbf{g}}_{\sigma_{\hat{g}}}$ = a vector of m known EBVs or GEBVs divided by its standard deviation in the whole population,

$b_{\sigma_{\hat{g}_i}}$ = an index coefficient of Ic1 for the ith trait (i = 1, , , , m) to be computed,

$\mathbf{b}_{\sigma_{\hat{g}}}$ = a vector of m unknown index coefficients of I_{c1} to be computed,

$\hat{\mathbf{g}}_{\sigma_g}$ = a vector of m known EBVs or GEBVs ($\hat{g}_i$) divided by the true genetic standard deviation for each trait (σ_{g_i}),

$b_{\sigma_{g_i}}$ = an index coefficient of I_{c2} for the ith trait (i = 1, , , , m) to be computed,

$\mathbf{b}_{\sigma_g}$ = a vector of m unknown index coefficients of I_{c2} to be computed,

g_i = an unknown genetic value for the ith trait,

$\mathbf{g}_{\sigma_g}$ = a vector of m unknown genetic values divided by the true genetic standard deviation for each trait (σ_{g_i}), and

H = originally called the "aggregate genotype" [3].

Economic values (**a**) are often used directly as the practical index coefficients of I_p [1,2]. Index coefficients ($\mathbf{b}_{\sigma_{\hat{g}}}$) of I_{c1} composed from the standardized trait ($\frac{\hat{g}_i}{\sigma_{\hat{g}_i}}$) were derived according to the method of [3]. The covariance of GEBV or EBV between two traits was based on the work of [7]. That is,

$$\sigma_{\hat{g}_i \hat{g}_j} = r_{\hat{g}_i} r_{\hat{g}_j} r_{G_{ij}} \sigma_{\hat{g}_i} \sigma_{\hat{g}_j},$$

where

$r_{\hat{g}_i}$ = the accuracy of the EBV or GEBV for trait i, and

$r_{G_{ij}}$ = the genetic correlation between traits i and j.

The equation for the selection index (I_{c1}) is

$$\begin{bmatrix} 1 & r_{\hat{g}_1} r_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_1} r_{\hat{g}_3} r_{G_{13}} & . & r_{\hat{g}_1} r_{\hat{g}_m} r_{G_{1m}} \\ r_{\hat{g}_2} r_{\hat{g}_1} r_{G_{21}} & 1 & r_{\hat{g}_2} r_{\hat{g}_3} r_{G_{23}} & . & r_{\hat{g}_2} r_{\hat{g}_m} r_{G_{2m}} \\ r_{\hat{g}_3} r_{\hat{g}_1} r_{G_{31}} & r_{\hat{g}_3} r_{\hat{g}_2} r_{G_{32}} & 1 & . & r_{\hat{g}_3} r_{\hat{g}_m} r_{G_{3m}} \\ . & . & . & . & . \\ r_{\hat{g}_m} r_{\hat{g}_1} r_{G_{m1}} & r_{\hat{g}_m} r_{\hat{g}_2} r_{G_{m2}} & r_{\hat{g}_m} r_{\hat{g}_3} r_{G_{m3}} & . & 1 \end{bmatrix} \begin{bmatrix} b_{\sigma_{\hat{g}1}} \\ b_{\sigma_{\hat{g}2}} \\ b_{\sigma_{\hat{g}3}} \\ . \\ b_{\sigma_{\hat{g}m}} \end{bmatrix}$$

$$= \begin{bmatrix} r_{\hat{g}_1} & r_{\hat{g}_1} r^2_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_1} r^2_{\hat{g}_3} r_{G_{13}} & . & r_{\hat{g}_1} r^2_{\hat{g}_m} r_{G_{1m}} \\ r^2_{\hat{g}_1} r_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_2} & r_{\hat{g}_2} r^2_{\hat{g}_3} r_{G_{23}} & . & r_{\hat{g}_2} r^2_{\hat{g}_m} r_{G_{2m}} \\ r^2_{\hat{g}_1} r_{\hat{g}_3} r_{G_{13}} & r^2_{\hat{g}_2} r_{\hat{g}_3} r_{G_{23}} & r_{\hat{g}_3} & . & r_{\hat{g}_3} r^2_{\hat{g}_m} r_{G_{3m}} \\ . & . & . & . & . \\ r^2_{\hat{g}_1} r_{\hat{g}_m} r_{G_{1m}} & r^2_{\hat{g}_2} r_{\hat{g}_m} r_{G_{2m}} & r^2_{\hat{g}_3} r_{\hat{g}_m} r_{G_{3m}} & . & r_{\hat{g}_m} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ . \\ a_m \end{bmatrix}$$

$$= \begin{bmatrix} 1 & r_{\hat{g}_1} r_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_1} r_{\hat{g}_3} r_{G_{13}} & . & r_{\hat{g}_1} r_{\hat{g}_m} r_{G_{1m}} \\ r_{\hat{g}_2} r_{\hat{g}_1} r_{G_{21}} & 1 & r_{\hat{g}_2} r_{\hat{g}_3} r_{G_{23}} & . & r_{\hat{g}_2} r_{\hat{g}_m} r_{G_{2m}} \\ r_{\hat{g}_3} r_{\hat{g}_1} r_{G_{31}} & r_{\hat{g}_3} r_{\hat{g}_2} r_{G_{32}} & 1 & . & r_{\hat{g}_3} r_{\hat{g}_m} r_{G_{3m}} \\ . & . & . & . & . \\ r_{\hat{g}_m} r_{\hat{g}_1} r_{G_{m1}} & r_{\hat{g}_m} r_{\hat{g}_2} r_{G_{m2}} & r_{\hat{g}_m} r_{\hat{g}_3} r_{G_{m3}} & . & 1 \end{bmatrix} \begin{bmatrix} r_{\hat{g}_1} a_1 \\ r_{\hat{g}_2} a_2 \\ r_{\hat{g}_3} a_3 \\ . \\ r_{\hat{g}_m} a_m \end{bmatrix}.$$

Therefore,

$$\begin{bmatrix} b_{\sigma_{\hat{g}1}} \\ b_{\sigma_{\hat{g}2}} \\ b_{\sigma_{\hat{g}3}} \\ . \\ b_{\sigma_{\hat{g}m}} \end{bmatrix} = \begin{bmatrix} r_{\hat{g}_1} a_1 \\ r_{\hat{g}_2} a_2 \\ r_{\hat{g}_3} a_3 \\ . \\ r_{\hat{g}_m} a_m \end{bmatrix} \quad \text{and}$$

$$I_{c1} = \sum_{i=1}^{m} r_{\hat{g}_i} a_i \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} \neq \sum_{i=1}^{m} a_i \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} = I_p \, .$$

In the same way as for the index equation of I_{c1}, the theoretically correct index coefficients of I_{c2} were derived according to the method of [3]. That is,

$$\begin{bmatrix} b_{\sigma_{g1}} & b_{\sigma_{g2}} & b_{\sigma_{g3}} & . & b_{\sigma_{gm}} \end{bmatrix} = \begin{bmatrix} a_1 & a_2 & a_3 & . & a_m \end{bmatrix}' \quad \text{and}$$

$$I_{c2} = \sum_{i=1}^{m} a_i \frac{\hat{g}_i}{\sigma_{g_i}} \, .$$

Note that

$$I_{c1} = \sum_{i=1}^{m} b_{\sigma_{\hat{g}_i}} \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} = \sum_{i=1}^{m} r_{\hat{g}_i} a_i \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} = \sum_{i=1}^{m} \frac{\sigma_{\hat{g}_i}}{\sigma_{g_i}} a_i \frac{\hat{g}_i}{\sigma_{\hat{g}_i}} = \sum_{i=1}^{m} a_i \frac{\hat{g}_i}{\sigma_{g_i}} = I_{c2} \, .$$

Because the practical selection is expressed as $I_p = \sum_{i=1}^{m} a_i \frac{\hat{g}_i}{\sigma_{\hat{g}_i}}$, practical selection ignores the individual accuracy for each trait and assumes that the accuracy is equal to unity for all traits. The economic value of a trait (a_i) multiplied by the accuracy of the evaluation of the trait ($r_{\hat{g}_i}$) is the correct coefficient for the practical index (I_p). In contrast, in practical selection, the economic value of a trait (a_i) is mistakenly used directly as an index coefficient of the ith standardized trait ($\frac{\hat{g}_i}{\sigma_{\hat{g}_i}}$) of I_p.

Economic values in retrospect for erroneous practical selection

The economic values in retrospect for erroneous selection using the practical index (I_p) were determined according to the theory on the index in retrospect [8,9]. The economic values in retrospect are

$$\mathbf{P}\mathbf{b}^* = \mathbf{G}\mathbf{a}^*,$$

where

b^* = a vector of the erroneous practical index weights,

$\mathbf{P}$ = an (m×m) covariance matrix of $\hat{\mathbf{g}}_{\sigma_{\hat{g}}}$,

$\mathbf{G}$ = an (m×m) genetic covariance matrix between $\hat{\mathbf{g}}_{\sigma_{\hat{g}}}$ and g_{σ_g}, i.e., $\mathrm{Cov}(\hat{\mathbf{g}}_{\sigma_{\hat{g}}}, \mathbf{g}_{\sigma_g}) = \mathbf{G}$, and

$\mathbf{a}^*$ = the economic weights in retrospect.

The economic values ($\mathbf{a}$) are used directly as index coefficients in selection using the practical index (I_p). Then

$$\begin{bmatrix} 1 & r_{\hat{g}_1} r_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_1} r_{\hat{g}_3} r_{G_{13}} & . & r_{\hat{g}_1} r_{\hat{g}_m} r_{G_{1m}} \\ r_{\hat{g}_2} r_{\hat{g}_1} r_{G_{21}} & 1 & r_{\hat{g}_2} r_{\hat{g}_3} r_{G_{23}} & . & r_{\hat{g}_2} r_{\hat{g}_m} r_{G_{2m}} \\ r_{\hat{g}_3} r_{\hat{g}_1} r_{G_{31}} & r_{\hat{g}_3} r_{\hat{g}_2} r_{G_{32}} & 1 & . & r_{\hat{g}_3} r_{\hat{g}_m} r_{G_{3m}} \\ . & . & . & . & . \\ r_{\hat{g}_m} r_{\hat{g}_1} r_{G_{m1}} & r_{\hat{g}_m} r_{\hat{g}_2} r_{G_{m2}} & r_{\hat{g}_m} r_{\hat{g}_3} r_{G_{m3}} & . & 1 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ . \\ a_m \end{bmatrix}$$

$$= \begin{bmatrix} r_{\hat{g}_1} & r_{\hat{g}_1} r_{\hat{g}_2}^2 r_{G_{12}} & r_{\hat{g}_1} r_{\hat{g}_3}^2 r_{G_{13}} & . & r_{\hat{g}_1} r_{\hat{g}_m}^2 r_{G_{1m}} \\ r_{\hat{g}_1}^2 r_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_2} & r_{\hat{g}_2} r_{\hat{g}_3}^2 r_{G_{23}} & . & r_{\hat{g}_2} r_{\hat{g}_m}^2 r_{G_{2m}} \\ r_{\hat{g}_1}^2 r_{\hat{g}_3} r_{G_{13}} & r_{\hat{g}_2}^2 r_{\hat{g}_3} r_{G_{23}} & r_{\hat{g}_3} & . & r_{\hat{g}_3} r_{\hat{g}_m}^2 r_{G_{2m}} \\ . & . & . & . & . \\ r_{\hat{g}_1}^2 r_{\hat{g}_m} r_{G_{1m}} & r_{\hat{g}_2}^2 r_{\hat{g}_m} r_{G_{2m}} & r_{\hat{g}_3}^2 r_{\hat{g}_m} r_{G_{3m}} & . & r_{\hat{g}_m} \end{bmatrix} \begin{bmatrix} a_1^* \\ a_2^* \\ a_3^* \\ . \\ a_m^* \end{bmatrix}$$

$$= \begin{bmatrix} 1 & r_{\hat{g}_1} r_{\hat{g}_2} r_{G_{12}} & r_{\hat{g}_1} r_{\hat{g}_3} r_{G_{13}} & . & r_{\hat{g}_1} r_{\hat{g}_m} r_{G_{1m}} \\ r_{\hat{g}_2} r_{\hat{g}_1} r_{G_{21}} & 1 & r_{\hat{g}_2} r_{\hat{g}_3} r_{G_{23}} & . & r_{\hat{g}_2} r_{\hat{g}_m} r_{G_{2m}} \\ r_{\hat{g}_3} r_{\hat{g}_1} r_{G_{31}} & r_{\hat{g}_3} r_{\hat{g}_2} r_{G_{32}} & 1 & . & r_{\hat{g}_3} r_{\hat{g}_m} r_{G_{3m}} \\ . & . & . & . & . \\ r_{\hat{g}_m} r_{\hat{g}_1} r_{G_{m1}} & r_{\hat{g}_m} r_{\hat{g}_2} r_{G_{m2}} & r_{\hat{g}_m} r_{\hat{g}_3} r_{G_{m3}} & . & 1 \end{bmatrix} \begin{bmatrix} r_{\hat{g}_1} a_1^* \\ r_{\hat{g}_2} a_2^* \\ r_{\hat{g}_3} a_3^* \\ . \\ r_{\hat{g}_m} a_m^* \end{bmatrix} .$$

Therefore

$$\begin{bmatrix} a_1^* \\ a_2^* \\ a_3^* \\ . \\ a_m^* \end{bmatrix} = \begin{bmatrix} \frac{a_1}{r_{\hat{g}_1}} \\ \frac{a_2}{r_{\hat{g}_2}} \\ \frac{a_3}{r_{\hat{g}_3}} \\ . \\ \frac{a_m}{r_{\hat{g}_m}} \end{bmatrix} .$$

By this reasoning, the economic weight in retrospect ($\mathbf{a}^*$) that is based on the practical index (I_p) is the economic value divided by its accuracy ($\frac{a_i}{r_{\hat{g}_i}}$); this results in an economic weight in retrospect that is relatively greater than the economic value ($\mathbf{a}$) for low-accuracy traits but that is relatively lower than the economic value ($\mathbf{a}$) for high-accuracy traits. The relative economic weight in retrospect for the ith trait ($a_{rel_i}^*$) can be written as

$$a_{rel_i}^* = \frac{\frac{|a_i|}{r_{\hat{g}_i}}}{\sum_{i=1}^{m} \frac{|a_i|}{r_{\hat{g}_i}}} \, .$$

Selection responses using the erroneous practical selection index

When selection is based on the erroneous practical selection index (I_p), the expected genetic response to the ith trait ($\Delta G_{i/I_p}$)

of net merit (H) is

$$\Delta G_{i/Ip} = \text{cov}(g_i, \sum_{j=1}^{m} a_j \frac{\hat{g}_j}{\sigma_{\hat{g}_j}}) \frac{\bar{i}}{\sigma_{Ip}}$$

$$= (a_i \sigma_{\hat{g}_i} + \sum_{j \neq i}^{m} a_j r_{\hat{g}_i} r_{\hat{g}_j} r_{G_{ij}} \sigma_{\hat{g}_i}) \frac{\bar{i}}{\sigma_{Ip}}$$

Where,

$$\sigma_{Ip}^2 = \sum_{i=1}^{m} a_i^2 + 2\sum_{i=1}^{m}\sum_{j \neq i}^{m} a_i a_j r_{\hat{g}_i} r_{\hat{g}_j} r_{G_{ij}} \quad \text{and}$$

$\bar{i}$ = selection intensity (or the standardized selection differential).

When selection is based on the theoretically correct selection index (I_{c1}), the expected genetic response to the ith trait ($\Delta G_{i/I_{c1}}$) of net merit (H) is

$$\Delta G_{i/Ic_1} = \text{cov}(g_i, \sum_{j=1}^{m} a_j r_{\hat{g}_j} \frac{\hat{g}_j}{\sigma_{\hat{g}_j}}) \frac{\bar{i}}{\sigma_{Ic_1}}$$

$$= (a_i r_{\hat{g}_i} \sigma_{\hat{g}_i} + \sum_{j=1, \neq i}^{m} a_j r_{\hat{g}_i} r_{\hat{g}_j}^2 r_{G_{ij}} \sigma_{\hat{g}_i}) \frac{\bar{i}}{\sigma_{Ic1}}$$

Where,

$$\sigma_{I_{c1}}^2 = \sum_{i=1}^{m} r_{\hat{g}_i}^2 a_i^2 + 2\sum_{i=1}^{m}\sum_{j>i}^{m} a_i a_j r_{\hat{g}_i}^2 r_{\hat{g}_j}^2 r_{G_{ij}}.$$

Because the selection indices I_{c1} and I_{c2} are the same index, the expected genetic responses due to I_{c1} and I_{c2} are the same.

Comparison of selection indices in terms of economic values in retrospect and selection responses

Let us assume that the net merit or "aggregate genotype" (H_1) is determined by the three traits of milk protein yield (MP), feet and legs score (FL), and somatic cell count (SCS), along with their economic values ($\mathbf{a}_3$). That is,

$$H_1 = 7.0\frac{G_1}{\sigma_{G_1}} + 1.8\frac{G_2}{\sigma_{G_2}} - 1.2\frac{G_3}{\sigma_{G_3}},$$

where $\mathbf{a}_3' = (7.0 \quad 1.8 \quad -1.2)$.

Next, let us consider the net merit in Japan, or as represented in the Nippon total profit index (H_2), along with their economic values ($\mathbf{a}_7$). That is,

$$H_2 = 7.0\left[\frac{38G_4}{\sigma_{G_4}} + \frac{62G_1}{\sigma_{G_1}}\right] + 1.8\left[\frac{32G_2}{\sigma_{G_2}} + \frac{68G_5}{\sigma_{G_5}}\right] + 1.2\left[\frac{-33G_3}{\sigma_{G_3}} + \frac{17G_6}{\sigma_{G_6}} + \frac{-50G_7}{\sigma_{G_7}}\right],$$

where

G_1 = true genetic value for milk protein yield,
G_2 = true genetic value for feet and legs score,
G_3 = true genetic value for SCS,
G_4 = true genetic value for milk fat yield,
G_5 = true genetic value for udder composite score,
G_6 = true genetic value for lactation persistency,
G_7 = true genetic value for days open,
σ_{G_i} = true genetic standard deviation for ith trait, and
$a_7' = (7\times38 \quad 7\times62 \quad 1.8\times32 \quad 1.8\times68 \quad 1.2\times(-33) \quad 1.2\times17 \quad 1.2\times(-50))$.

The practical but erroneous indices of I_1 and I_2 are taken for H_1 and H_2, respectively. The economic weight for each trait is used directly as the coefficient of the standardized component trait; that is,

$$I_1 = 7.0\frac{\hat{G}_1}{\sigma_{\hat{G}_1}} + 1.8\frac{\hat{G}_2}{\sigma_{\hat{G}_2}} + 1.2\frac{\hat{G}_3}{\sigma_{\hat{G}_3}}, \text{ and}$$

$$I_2 = 7.0\left[\frac{38\hat{G}_4}{\sigma_{\hat{G}_4}} + \frac{62\hat{G}_1}{\sigma_{\hat{G}_1}}\right] + 1.8\left[\frac{32\hat{G}_2}{\sigma_{\hat{G}_2}} + \frac{68\hat{G}_5}{\sigma_{\hat{G}_5}}\right] + 1.2\left[\frac{-33\hat{G}_3}{\sigma_{\hat{G}_3}} + \frac{17\hat{G}_6}{\sigma_{\hat{G}_6}} + \frac{-50\hat{G}_7}{\sigma_{\hat{G}_7}}\right].$$

On the other hand, the theoretically correct indices are

$$I_1^* = 7.0\frac{\hat{G}_1}{\sigma_{G_1}} + 1.8\frac{\hat{G}_2}{\sigma_{G_2}} + 1.2\frac{\hat{G}_3}{\sigma_{G_3}} \quad \text{and}$$

$$I_2^* = 7.0\left[\frac{38\hat{G}_4}{\sigma_{G_4}} + \frac{62\hat{G}_1}{\sigma_{G_1}}\right] + 1.8\left[\frac{32\hat{G}_2}{\sigma_{G_2}} + \frac{68\hat{G}_5}{\sigma_{G_5}}\right] + 1.2\left[\frac{-33\hat{G}_3}{\sigma_{G_3}} + \frac{17\hat{G}_6}{\sigma_{G_6}} + \frac{-50\hat{G}_7}{\sigma_{G_7}}\right].$$

We compared economic weights and selection responses between the practical and theoretical indices for the two examples of net merit (H_1 and H_2). Furthermore, four scenarios of reliability were assumed for GEBV in the component traits of practical and theoretical indices for I_1 and I_1^* under the net merit H_1. Selection responses from I_1 and I_1^* were then compared under four scenarios of reliability, i.e., 1) the reliability for MP was twice that for the present situation, but the reliabilities for FL and SCS were the same as currently; 2) reliability for MP was half that of the present situation but those for FL and SCS were the same as currently; 3) reliabilities for FL and SCS were twice those of the present situation but that for MP was the same as currently; and 4) reliabilities for FL and SCS were half those of the present situation but that for MP was the same as currently. The selection intensity was set to unity ($\bar{i}$ = 1) for all selection criteria so that selection responses could be compared. The genetic covariances of the component traits of the selection indices used were obtained from [1]. The reliabilities of the component traits of selection indices for dairy cow EBV and GEBV in the whole population in Japan were obtained from [1].

RESULTS AND DISCUSSION

The expected selection responses and economic weights from the practical (I_1) and theoretical (I_1^*) indices for net merit (H_1), composed of MP, FL, and SCS, are shown (Table 1). The economic weights in retrospect for the practical index (I_1) are the relative economic weights ($a^*_{rel_i}$) as shown in Materials and Methods, and the economic weights for the theoretical index (I_1^*) are the known economic values ($\mathbf{a}_3$). The selection response to FL from the practical index (I_1) based on dairy cow EBV, which did not account for reliability, was 1.56 times greater than that from the theoretical index (I_1^*). In contrast, the response to MP from the practical index (I_1) based on dairy cow EBV was 0.98 times that from the theoretical index. On the basis of dairy cow EBV, the accuracy of FL was the lowest, and that of MP was the highest, among the three traits in the index investigated. Similarly, on the basis of GEBV, the ratio of the response from the practical index to that from the theoretical index was the lowest for SCS (which had the highest accuracy) and the highest for MP, which had the lowest accuracy among the three traits in the index investigated. However the difference between the highest and lowest ratios based on GEBV was smaller than that based on dairy cow EBV, because the difference between the highest and lowest accuracies based on GEBV was smaller than that based on dairy cow EBV. Thus, the selection response associated with use of the practical index (I_1), which did not account for reliability, was overestimated for a trait for which the evaluation accuracy (EBV or GEBV) was lower than those of the other traits in the index and was underestimated for a trait for which the evaluation accuracy was higher than those of the other traits in the index. However, the magnitude of the over- or under-estimation of the selection response differed according to the extent of the difference between the accuracies of the traits in the index.

The economic weight of each trait in retrospect associated with use of the practical index (I_1) is the economic weight of the trait divided by its accuracy. Therefore, as shown (Table 1), the economic weights in retrospect that did not account for reliability (I_1) were greater than the known economic weights in the theoretical index (I_1^*) for traits where the accuracy of the evaluation (EBV or GEBV) was lower than those of the other trait evaluations. Regardless of whether the reliability of trait evaluations was included or ignored, the objective of selection indices I_1 and I_1^* was to improve net merit (H_1). However, the economic weight in retrospect for the ith trait from the practical index (I_1) was not the economic value (a_i) but rather the economic value divided by its accuracy ($\frac{a_i}{r_{\hat{g}_i}}$). Therefore, a practical selection index aims to increase the value of $\frac{a_i}{r_{\hat{g}_i}}$. Thus, compared with the theoretical index (I_1^*), the practical index (I_1) overestimated the economic weights and selection responses associated with low-accuracy traits within the index and underestimated those for high-accuracy component traits. For example, the relative economic weight in retrospect ($a^*_{rel_i}$) associated with the practical index (I_1) for MP based on dairy cow EBV was 0.65, compared with the correct economic weight of 0.7, because the accuracy of evaluation of MP was the highest among the three traits in the index.

The variance of EBVs changes every time the breeding values in the whole population are computed, because data are accumulated during every computation. As a result, realized reliability differs every time breeding value is computed. Thus, economic weight in retrospect associated with use of the practical index (I_1), which is expressed as the economic value of the trait divided by its accuracy, differs every time breeding value is computed or every selection, whereas the correct economic weight of the trait should remain the same every time breeding value is computed or every selection. In practice, breeding is undertaken to accomplish a definite goal in each population. Selection is used to maximize net merit or achieve the breeding goal, but the net merit or breeding goal at which the practical selection index (I_1) is aimed changes every time breeding value is computed or every selection, thus slowing genetic improvement.

The ratios of selection responses from the practical index to those from the theoretical index under the four scenarios of altered

Table 1. Selection responses and economic weights obtained by using practical and theoretical indices for GEBV and dairy cow EBV

Selection response[1)]	GEBV				Dairy cow EBV			
	I_1*[2)]	I_1[3)]	Ratio (I_1/I_1^*)	Accuracy	I_1^*[2)]	I_1[3)]	Ratio (I_1/I_1^*)	Accuracy
MP	0.5025	0.5041	1.0033	0.5292	0.7274	0.7141	0.9817	0.7503
FL	0.1029	0.1006	0.9778	0.5385	0.0575	0.0894	1.5558	0.5899
SCS	–0.0894	–0.0831	0.9289	0.5657	–0.0609	–0.0816	1.3401	0.5992
Economic weight								
MP	0.7000	0.7077	1.011	0.5292	0.7000	0.6486	0.9266	0.7503
FL	0.1800	0.1788	0.9934	0.5385	0.1800	0.2121	1.1786	0.5899
SCS	–0.1200	–0.1135	0.9457	0.5657	–0.1200	–0.1392	1.1604	0.5992

GEBV, genomically enhanced breeding value; EBV, estimated breeding value; MP, milk protein yield; FL, feet and legs score; SCS, somatic cell score.
[1)] Unit = genetic standard deviation. [2)] Theoretical selection index. [3)] Practical selection index.

and current reliabilities are shown (Figure 1). Milk protein yield had the greatest economic weight of 0.7, whereas FL and SCS had lower weights of 0.18 and –0.12, respectively. Reliability for MP was set as double the original value in scenario 1 and as half the original value in scenario 2. Reliabilities for FL and SCS were set to double the original values in scenario 3 and to half the original values in scenario 4. Figure 1 reveals the same trend as that seen (Table 1), with overestimation of selection responses associated with low-accuracy traits within the index and underestimation of those for high-accuracy component traits. The ratios for MP under the four scenarios of altered and current reliabilities ranged from 0.98 to 1.05, whereas those for SCS and FL ranged from 0.66 to 1.43 and from 0.68 to 1.80, respectively. That is, the over- or under-estimation of selection responses recognized (Table 1) was more marked for SCS and FL than for MP. This finding indicated that the magnitude of the over- or under-estimation in selection responses was greater for SCS and FL, for which the economic weights were lower than those of the other traits in the index, and that selection responses were comparatively stable for MP, which received greater economic weight than did the other traits in the index. That is, the use of the practical selection procedure or of inaccurate economic weights had a greater effect on traits with relatively low economic weights within the index than on traits with greater economic weights.

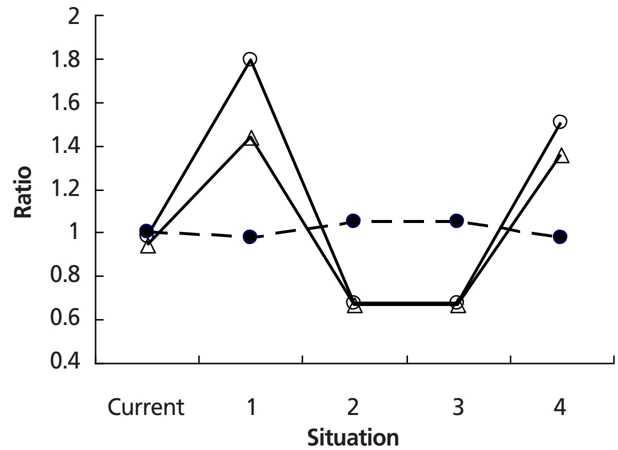

Figure 1. The ratios of selection responses from the practical index to those from the theoretical index under the four scenarios of altered and current reliabilities (1 = reliability was set as double the current value for MP, 2 = reliability was set as half the current value for MP, 3 = reliability was set to double the current value for FL and SCS, 4 = reliability was set to half the current value for FL and SCS). ---●---, milk protein yield (MP); —○—, feet and legs (FL); —Δ—, somatic cell score (SCS).

The expected selection responses and economic weights from the practical (I_2) and theoretical (I_2^*) indices for net merit or the Nippon total profit index (H_2) composed of milk protein yield, feet and legs score, SCS, milk fat yield, udder composite score, lactation persistency, and days open are shown (Table 2). As recognized (Table 1), over-estimation of selection responses associated with low-accuracy traits within the index and under-estimation of those for high-accuracy component traits were recognized (Table 2). For example, udder composite score, which had the greatest accuracy on GEBV, showed the greatest under-estimation of selection response associated with use of the practical index (I_2), and SCS, which had a fairly low economic weight and accuracy on dairy cow EBV, showed the greatest over-estimation of selection response associated with use of the practical index (I_2). The covariance of GEBV or EBV between two traits ($\sigma_{\hat{g}_1\hat{g}_2}$), from the work of [9], can be written as $r_{\hat{g}_1}^2 r_{\hat{g}_2}^2 \sigma_{g_1 g_2}$. Thus, the selection response for each trait is affected not only by its accuracy but

Table 2. Selection responses and economic weights obtained by using practical and theoretical indices for GEBV and dairy cow EBV in total net merit (NTP)

Items	Selection response[1)]				Economic weight		
	Accuracy	I_2^{*}[2)]	I_2[3)]	Ratio (I_2/I_2^*)	I_2^{*}[2)]	I_2[3)]	Ratio (I_2/I_2^*)
GEBV							
Milk fat yield	0.5831	0.00358	0.00344	0.9520	0.26600	0.25723	0.9670
Milk protein yield	0.5292	0.00438	0.00449	1.0164	0.43400	0.46247	1.0656
Feet and legs score	0.5385	0.00026	0.00024	0.9252	0.06300	0.06596	1.0471
Udder composite	0.6689	0.00163	0.00115	0.7066	0.11700	0.09919	0.8477
Days open	0.6481	–0.00057	–0.00050	0.8774	–0.06000	–0.05220	0.8701
Somatic cell score	0.5657	–0.00039	–0.00036	0.9124	–0.03960	–0.03947	0.9968
Lactation persistency	0.4899	0.00016	0.00018	1.1279	0.02040	0.02348	1.1510
Dairy cow EBV							
Milk fat yield	0.7700	0.00533	0.00518	0.9717	0.26600	0.24683	0.9279
Milk protein yield	0.7503	0.00665	0.00657	0.9882	0.43400	0.41331	0.9523
Feet and legs score	0.5899	0.00005	0.00006	1.1482	0.06300	0.07631	1.2113
Udder composite	0.6874	0.00190	0.00260	1.3678	0.11700	0.12229	1.0452
Days open	0.5762	–0.00088	–0.00103	1.1776	–0.06000	–0.07441	1.2401
Somatic cell score	0.5992	–0.00019	–0.00030	1.5192	–0.03960	–0.04723	1.1926
Lactation persistency	0.7423	0.00018	0.00022	1.2243	0.02040	0.01964	0.9626

GEBV, genomically enhanced breeding value; EBV, estimated breeding value.
[1)] Unit = genetic standard deviation. [2)] Theoretical selection index. [3)] Practical selection index.

also by the accuracies of the other traits in the index. Therefore, the trend recognized (Table 1) regarding the over-estimation of selection responses associated with low-accuracy traits within the index and the under-estimation of those for high-accuracy component traits would be ameliorated as the number of traits included in an index increased.

However, for all of traits in the index (regardless of their number), use of a practical selection index leads to inaccurate economic weights and, consequently, delays in genetic improvement. In a previous study, the reliabilities of genomic predictions for 26 milk yield and conformation traits varied from 33% to 69% [10]. That is, the maximum difference between the accuracies of the component traits in a selection index determines the degree of inaccuracy in the calculated economic values and selection responses, such that the error in estimation is minimized when all of the component traits in an index are equivalent in accuracy. However, selection that accounts for reliability remains important, especially when the reliabilities of component traits of an index vary widely. A selection index and net merit may or may not include the same traits, and the selection index equation needs to be extended to accommodate the different numbers of traits included in the selection index and in the net merit.

CONFLICT OF INTEREST

We certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

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