Measuring the effect of change in selection indices

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ABSTRACT

Genetic selection goals for dairy cattle, originally aimed at production traits only, have been expanded in stages over the past 30 yr to include up to 12 target traits covering production, functionality, and health and fertility. Each addition to the selection goal often involves the use of additional measured phenotypic variates. The net effect of these additions is usually described as causing change in the relative emphasis on different traits, though there are varying definitions of what this means. This paper suggests that the current definitions of this term may be inappropriate and shows that, as usually used, it tends to overstate the net effect of the changes. A new definition of the relative emphasis of each target trait is proposed. It is defined as the percentage of total economic value of genetic gain in all traits attributable to gain in that particular trait. A useful parallel statistic measures the relative contribution of each phenotypic variate recorded. The result of applying these measures is contrasted with the use of current methods using United States Holstein data.

Key words: selection index, relative emphasis, relative contribution

INTRODUCTION

The original formulation of selection index theory (Hazel, 1943) distinguished clearly between the aggregate genotype, which is composed of a (usually linear) combination of genotypic values of the candidates for selection (i.e., target traits), and the selection index (**SI**), which is a linear combination of phenotypic variates measured on those candidates, their relatives, or both (i.e., measured variates). Over the years, methods of calculation and statistical models representing phenotypic data have become more sophisticated. Terminology has also changed. However, the essential distinction remains between the defined aggregate genotype, now called total economic merit (**TEM**; Shook, 2006), and the calculated SI.

Changes can be made in the definition of TEM by adding or deleting traits and by altering their preassigned economic values. Changes will also result from the addition or deletion of measured phenotypic variates in the SI. The implementation of changes in either case will alter the amount of genetic gain resulting from selection, as well as its distribution over the target traits. However, there is an important distinction. Changes made in the TEM incur no direct costs. They may, however, have consequential costs (or gains) in terms of the amount and kind of genetic change achieved. These consequences are of major interest to dairy producers, typically the clients of an AI company. Change in the measured variates used in the SI, on the other hand, has both direct and consequential cost implications. Additional expenditure is required, for example, to record SCS in daughter groups. These consequences are of primary interest to those financing the breeding program, typically the AI company. Investment in a selection program therefore requires careful calculation and balancing of the costs and consequences of changes to both the TEM and the SI.

Because dairy cattle SI have evolved over the last 30 yr, it has generally been the case that the addition of new traits to the TEM has been accompanied by the recording of new variates in the SI. This simultaneous addition of new target traits and corresponding measured variates has led to some lack of clarity about the different consequences of adding new traits or variates. Traits that might or might not be included in the TEM will change as correlated responses even if corresponding variates have not been measured. Until recently these correlated (and generally negative) responses were not calculated. The total economic value of genetic change achieved was therefore overestimated.

Apart from the calculation of overall economic gains from selection, there is considerable interest in the way in which changes in the TEM or the SI affect the distribution of total gains over the various target traits. The most frequently used term to describe this is the change in the “relative emphasis” this produces for the different traits. The term seems to have been used first by Leitch (1994). The method of calculation was not given, but it was stated as “relative emphasis on traits

Received July 31, 2007.

Accepted August 31, 2009.

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after accounting for differences in standard deviations of genetic evaluations." Relative emphasis was given as a percentage, with absolute (i.e., positive and negative) values summing to 100% across all traits. The paper concluded that failure to account for differences in standard deviations of genetic evaluations will lead to misleading interpretation of indices, and also that the actual relative emphasis on traits may be different based on correlations between traits.

Relative emphasis for a trait was defined by VanRaden (2002) as "economic value times standard deviation divided by the sum of the absolute values of these products, then multiplied by 100." The implicit assumption involved is that selection on the index produces equal genetic gain (in SD units) in all traits, which is clearly never the case. Miglior et al. (2005) used a similar definition, but dividing instead of multiplying economic values by standard deviations. The essential feature of both of these definitions is the attempt to standardize across traits (within countries) by multiplying (or dividing) the economic value per unit of each one by its genetic standard deviation and expressing the results as percentage of the sum of these products. Shook (2006) compared indices using the same statistic as VanRaden (2002), but using the term "relative economic weights," whereas the trade journal *Holstein International* (2006) compared indices across countries using a "composition of the total indices" measure that was not defined. Clearly, these different approaches to the same question are likely to give different results. In addition, the general term relative emphasis, although intuitively appealing, is impossible to relate either to the expenditure devoted to selection on particular traits or to the genetic and economic consequences of that selection.

Dairy farmers are concerned that the procedures used for evaluation of sires should consistently rank those sires correctly. For the overall selection objective, the TEM or SI evaluation does this. Secondary statistics derived from the SI, such as the new relative emphasis and the relative contribution measures proposed here, are consistent with this correct ranking. When sires are reranked for individual target traits (PTA), the rankings will change from trait to trait. There is no way to predict the reranking of a particular sire across his single-trait PTA from any version of relative emphasis. In fact, because PTA is single-trait selection with evaluation based on multiple measured variates, the concept of relative emphasis is not relevant.

The principal objective of the present study was to propose a new definition of relative emphasis that reflects the contribution that genetic change in each trait makes to the overall genetic gain from selection on

the index. This should correspond more closely to the interests of dairy producers.

MATERIALS AND METHODS

It is possible that more appropriate measures developed many years ago (Cunningham, 1969, 1970) give more meaningful results. First, it is necessary to distinguish again between target traits included in the TEM and measured variates included in the SI. An appropriate measure of the value of each trait included in the TEM can be calculated as the percentage of total economic value of genetic gain from selection on the index attributable to genetic change in that trait. This calculation is independent of whether or not a corresponding phenotypic measure has been included in the index. This, in effect, is a new definition of relative emphasis on each target trait.

The relative emphasis for the j th target trait is (Cunningham, 1970)

$$\frac{b'G_j}{b'Pb}(v_j)(100),$$

where P is the $(n \times n)$ phenotypic variance-covariance matrix for the n measured variates; G_j is the j th column of G , the $(n \times m)$ phenotypic $\times$ genotypic variance-covariance matrix linking the n measured variates and the m target traits; b is a vector of calculated index weights for the n measured variates; and v_j is the assigned relative economic weight for the j th target trait.

A parallel statistic can be calculated to describe the relative contribution of each measured variate. This is defined as the percentage reduction in total economic value of overall genetic gain if that particular variate is omitted from the index.

The relative contribution for the i th measured variate is (Cunningham, 1969)

$$100 - \sqrt{\frac{b_i'Pb - \frac{b_i^2}{P_{ii}^{-1}}}{b'Pb}}(100),$$

where b_i is the calculated index weight for the i th measured variate and P_{ii}^{-1} is the i th diagonal element of P^{-1} . This statistic is equivalent to the reduction in sums of squares because of a particular explanatory variate in an ANOVA.

The use of these measures of relative emphasis on target traits and relative contribution of measured variates is illustrated using the latest (June 2006) economic

Table 1. Traits included in this study¹

Group	Trait	Unit	Value (\$/target trait unit)	Year added
Production	Milk	Pounds	0	1971
	Fat	Pounds	2.70	1971
	Protein	Pounds	3.55	1976
Functionality	Size	Composite	-14	2000
	Udder	Composite	28	2000
	Legs and feet	Composite	13	2000
Health/fertility	Productive life (PL)	Months	29	1994
	SCS	Log of score	-150	1994
	Daughter pregnancy rate (DPR)	Percentage	21	2003
	Calving ability (CA)	Dollars	1	2003

¹Detailed definitions and derivation of economic values can be found in USDA (2006). Year of addition to USDA index is from VanRaden et al. (2004).

weights and genetic and phenotypic parameters for the United States Holstein population (USDA, 2006). Table 1 lists the 10 traits, the units in which they are measured, the value of each unit, and the year in which this trait was added to the index. They are separated into 3 groups: production, functionality, and health and fertility. These data were used to construct SI, assuming that all variates are measured on progeny groups of 75 daughters.

RESULTS AND DISCUSSION

The overall economic value of genetic gain from selection on any index is proportional to the standard deviation of the index. This in turn is a function of the target traits included in the TEM, the economic weights assigned to them, the measured variates used in constructing the index, and the 3 matrices of genetic and phenotypic covariances linking all of these together. Table 2 shows the relative gains from 3 indices that correspond approximately to the sequential development of the USDA index. The first index contains (as measured variates) production variates only, the second contains production and functionality variates, and the third contains production, functionality, and health and fertility variates.

Two versions of each index are used: (a) assuming only traits corresponding to measured variates are included in the TEM, and (b) where all 10 traits are included in the TEM, and where account is taken of the

economic consequences of correlated genetic responses in all traits.

In practice, with each expansion of the USDA index, the number of measured variates and target traits was increased in parallel. Thus, for index 1a, 3 production variates were measured and the same 3 traits were included in the TEM. For index 2a, 6 variates were measured and 6 corresponding target traits were included in the TEM. The second line in Table 2 shows the relative gains from 3 indices when change in all 10 target traits is accounted for.

The differences observed are small. This suggests that, with the parameters and economic weights used, the net penalty for using the simplest production-only index was small and the gain from adding 7 additional measured variates was also modest.

With the parameters used, the production-only index overstated the economic gain from selection by 4.4% because it did not take account of the negative genetic change in traits for which corresponding variates were not measured. Index 2, in which measured variates include functionality as well as production, recovers virtually all of this difference, whereas for index 3, in which all 10 traits have corresponding measured variates, there was an improvement of 3.4% in economic value of total gain.

Table 3 shows the relative emphasis on different target traits for the same 3 indices, again (a) ignoring or (b) accounting for correlated responses in traits for which no corresponding variate was measured.

Table 2. Relative gain from selection on 3 selection indices for (1) production only, (2) production + functionality, and (3) production + functionality + health and fertility

Total economic merit (TEM) includes ¹	Index 1	Index 2	Index 3
(a) Only traits corresponding to measured variates	100	99.9	103.4
(b) All 10 traits	95.6	100.2	103.4

¹Indices are calculated (a) assuming only traits corresponding to measured variates are included in TEM and (b) taking account of correlated responses in all traits.

Table 3. Relative emphasis on different target traits in 3 selection indices for (1) production only, (2) production + functionality, and (3) production + functionality + health and fertility¹

Trait	Index 1		Index 2		Index 3
	a ²	b ²	a	b	a, b
Milk	0	0	0	0	0
Fat	51.2	53.5	51.0	48.6	44.9
Protein	48.8	51.1	48.7	46.4	42.8
Size		1.2	2.1	2.6	2.4
Udder		-3.3	-1.8	-0.07	-0.03
Legs and feet		-0.1	0.07	0.26	0.2
Productive life		2.3		5.1	8.6
SCS		-2.7		-1.7	0.12
Daughter pregnancy rate		-3.0		-2.6	-1.3
Calving ability		1.1		1.4	2.2

¹Relative emphasis of a trait is defined as percent of total genetic gain from selection on the index attributable to genetic change in that trait.

²Relative emphasis is calculated (a) assuming only traits corresponding to measured variates are included in total economic merit and (b) taking account of correlated responses in all traits.

Under index 1 (selecting on production only), the correlated responses in the remaining 7 traits have relatively modest values in the index. Under indices 2 and 3, the relative value of these traits is generally enhanced, but not greatly. In all cases, the production traits fat and protein are overwhelmingly the most important. Productive life is the most important of the other 7 traits.

Table 4 shows a comparison of the old and new measures of the relative emphasis on different traits. These are compared for 2 indices. The first index corresponds to the MFP\$ (1976) index used by USDA. When importance is measured using the new definition of relative emphasis (i.e., the relative value of a trait in total economic value of genetic gain), it can be seen that fat contributes 51% and protein 49% of this gain. The old definition of relative emphasis gives values of 27% for milk, 46% for fat, and 27% for protein. However, the nature of that calculation presumes that one genetic standard deviation of gain is made in each trait. This clearly does not correspond to the actual gains made, which will vary from trait to trait, nor does it correspond to the economic benefit from selection on the index. It is therefore difficult to relate these figures either to the costs of the selection exercise or its economic consequences.

These 2 measures are again compared using index 3, which corresponds to the NM(\$\$) 2003 USDA index. For the production traits, the new relative emphasis measures are slightly reduced as the 7 additional traits enter the picture. For the old relative emphasis measure, protein has a higher percentage (33%) than fat (22%), reflecting a shift in economic value per kilogram. The old relative emphasis measure gives values ranging from 3 to 11% for the other 7 traits. Because this again assumes one standard deviation of gain in each trait, it

bears no relation to the consequences of using the index in practice. The new measure of relative emphasis, in contrast, shows a much more modest effect of including the 7 traits. When they are added as target traits to the selection goal, only 3 (size, productive life, and calving ability) make economically significant contributions.

In general, these results suggest that, by using the old relative emphasis approach, we have been overestimating the net genetic and economic consequences of the changes that have been made in dairy selection indices over the past 30 yr. The production traits protein and fat still dominate the value of target traits included in TEM.

The relative contributions of different measured variates for the 3 selection indices are shown in Table 5. The figures here are generally small. The greatest loss would be if fat were dropped from the list of measured variates. Despite the fact that it has lower economic weight than protein and similar heritability, the relative

Table 4. Comparison of new and old measures of relative emphasis on traits

Trait	Index 1 relative emphasis		Index 3 relative emphasis	
	New	Old ¹	New	Old
Milk	0	27	0	0
Fat	51	46	45	22
Protein	49	27	43	33
Size			2.4	-3
Udder			-0.03	7
Legs and feet			0.2	4
Productive life			8.6	11
SCS			0.12	-9
Daughter pregnancy rate			-1.3	7
Calving ability			2.2	-4

¹From VanRaden (2004), MFP\$ (1976), and NM\$ (2003).

Table 5. Relative contribution of different measured variates in 3 selection indices for (1) production only, (2) production + functionality, and (3) production + functionality + health and fertility¹

Trait	Index 1		Index 2		Index 3
	a ²	b ²	a	b	a,b
Milk	0.05	0.08	0.06	0.07	0.07
Fat	10.19	10.10	10.16	9.92	8.70
Protein	4.60	5.12	4.67	4.66	4.09
Size			0.79	2.18	0.96
Udder			0.77	3.15	1.02
Legs and feet			0.14	0.44	0.16
Productive life					0.91
SCS					0.30
Daughter pregnancy rate					0.11
Calving ability					0.43

¹Relative contribution of a variate is defined as percentage reduction in total genetic gain if that variate is omitted from the index.

²Relative contribution is calculated (a) assuming only traits corresponding to measured variates are included in total economic merit and (b) taking account of correlated responses in all traits.

contribution of fat is greater than the relative contribution of protein. This is largely because it has a higher standard deviation than protein. Because all traits, particularly the main production traits, are linked by strong genetic and phenotypic correlations, if any one is dropped from the list of measured variates, the reduction in total selection gain is relatively small. When included as measured variates, none of them adds more than 1% to the total economic value of selection.

CONCLUSIONS

Throughout the developed world, dairy cattle selection programs are planned and executed on the basis of SI methodology. These are constantly adapted, refined, and improved. Methods for monitoring and reporting the consequences of change are important both for program managers and for dairy farmers. For the latter group, the end users, the primary interest is in the contribution that change in each target trait makes to the overall economic gain from selection. The new relative emphasis statistic proposed here measures this precisely. It can be used for individual traits or for groups of traits as needed. It could be the preferred way to communicate the consequences of change in the selection goal. This is important also for program management and design. In addition, program managers need to be able to calculate the benefit derived from the inclusion or exclusion of particular measured variates in the index.

The parallel statistic, which we have called the relative contribution of each measured variate, can be used for this purpose. Taken together, these 2 statistics provide a comprehensive method for planning, measuring, and communicating change in selection programs.

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