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Present and Future Uses of Selection Index Methodology in Dairy Cattle

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ABSTRACT

Selection indexes have been extensively applied in the estimation of breeding value of dairy cattle for single traits as well as for combinations of traits for selection purposes. Milestones in methodology, such as multiple-trait evaluation procedures by BLUP, (co)variance component estimation, nonlinear models, discounted gene flow, dynamic programming, and international sire evaluations, together with increased computing power and the development of integrated AI and recording schemes, have contributed to efficient implementation of selection indexes and are reviewed in this article. Results of an international survey on evaluation practices and breeding programs are presented, demonstrating wide adoption of index selection for total merit and the need for further applications. Results from a simulation study on the efficiency of index selection for total merit are also presented; when the breeding goal includes, in addition to production traits, functional nonproduction traits such as mastitis resistance and fertility, failure to consider these traits in the selection index decreases efficiency 15 to 25%. Future applications are also discussed in view of advances in the areas of genome mapping, marker detection, and international comparisons. Further research should focus on functional nonproduction traits.

(**Key words**: selection index, total merit, dairy cattle)

Abbreviation key: **INTERBULL** = International Bull Evaluation Service, **TMI** = total merit index.

INTRODUCTION

"The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him." This citation from *The Origin of Species* by Charles Darwin (8) was given by L. N. Hazel as an introduction to his classic paper "The Genetic Basis for Constructing Selection Indexes" published 50 yr ago (12). Hazel's interpretation of this wise statement into constructive means for selection of farm animals has had a tremendous impact on efficiency of animal food production around the world.

Successful original research assumes both bright original ideas and the ability to clarify and develop these ideas into a greater understanding of a problem or into tools to exploit the knowledge for beneficial use. Certainly, the paper by Hazel (12) has very rightly been credited for introducing the formalized theory of selection index into animal breeding, as Smith (41) did for plant breeding. The primary idea presented by Hazel (12) was certainly not focused on the use of different sources of information for single-trait evaluations; rather, it emphasized the definition of multiple-trait breeding goals and objective means of assessing appropriate weights to the different traits being recorded, considering genetic relationships and variances and covariances among the traits included.

Although literature reviews on selection indexes almost always seem to refer to the Hazel (12) paper published in 1943, it could be argued that the basic idea of multiple-trait selection and the combination of several traits into a selection index had already been outlined in an earlier paper published the same year by Hazel and Lush (13). In their study of efficiency of three selection methods (tandem, total score, and independent culling), the authors discussed at length relative economic weighting of traits

and the construction of a "total score". Their conclusions seem to be as valid today as then: "selection for a total score or index of net desirability is much more efficient than selection for one trait at a time," and "selection on independent culling levels is less efficient than selection on total score but in some cases permits earlier selection without waiting until all traits are mature."

Many improvements in parameter estimation, breeding value calculation, and selection index derivation have, quite naturally, taken place during the past 50 yr. Our emphasis is on applications of the main scientific contribution of Hazel, namely, the idea of constructing multiple-trait indexes. A few developmental milestones, which lead to present applications, are also mentioned. A recent survey of selection index application in dairy cattle, including 28 countries around the world, is presented, and the importance of different groups of traits analyzed in dairy cattle. The latter also suggests future research priorities regarding dairy cattle selection.

METHODOLOGY MILESTONES

Developments in artificial breeding (first AI and freezing of semen and then multiple ovulation and embryo transfer) have increased the potential for genetic improvement and the demand for more sophisticated methods of genetic evaluation of animals and genetic parameter estimation. Over the years, particular emphasis has been placed on development of appropriate methodology to provide such tools for accurate and efficient selection.

Unlike the subjectivity and variability of breeding goal definition, estimation of genetic merit of animals for various traits finds common ground in almost all recording and evaluation philosophies. The global need is to apply methods to increase the reliability of evaluation and to utilize all possible information (data, genetic relationships, and correlations), to increase selection accuracy, to reduce generation interval, and finally to improve response to selection.

Phenotypic daughter averages and contemporary comparisons have gradually been replaced as evaluation methods by linear model techniques that reduce biases from the influence of environmental factors, selective sire mating, and nonrandom sire distribution across herds. The transition from the original evaluation methods to best linear prediction and BLUP has been well documented by Henderson (15, 16), whose mixed model equations relaxed the unrealistic assumption of the original selection index, that the means for comparison are estimated without error.

Among potential applications of BLUP, the sire, sire-maternal grandsire, and individual animal models have been the most popular. In fact, because of advances in computing and programming facilities, the animal model has rapidly gained acceptance as the most accurate evaluation method.

Hazel (12) defined phenotypic and genetic correlations that were needed for the construction of multiple-trait selection indexes and implied how they could be estimated. The development of methods for estimation of variances and covariances for unbalanced animal data (14, 29) provided the prerequisites for efficient simultaneous evaluation of correlated traits as reviewed by Meyer (27). Simultaneous genetic evaluation of many correlated traits has also been investigated as a means of improving the accuracy of evaluation of any single trait (17, 22). Additionally, multiple-trait approaches facilitate evaluations in cases of unrecorded or partially recorded traits. Reliable genetic correlations among traits are required for such evaluations. The complexity of this problem instigated research to simplify procedures for genetic parameter estimation (26). Gains from such results apply not only to accurate multiple-trait evaluation of animals but also to estimation of appropriate weights for selection index.

Extension of evaluation procedures to consider nonproduction traits has introduced the problem of analyzing categorical variates. Despite the linear model flexibility, pertinent assumptions were clearly violated when such data were offered for evaluation (10, 43). This difficulty led to the development of methods using nonlinear threshold models for sire evaluation and genetic parameter estimation (11), allowing more traits to be properly evaluated and setting new milestones in the quest for accurate selection.

A basic idea of the "total score", or selection index, was proposed to combine traits according to their economic importance. The area of deriving economic weights is under constant debate because of factors such as

variable planning horizons, target groups, and economic systems.

The development of nonlinear and restricted indexes, as well as desired gain indexes and derivation of weights to obtain predetermined goals for certain traits, were discussed in detail by Brascamp (3). Such approaches are essential for situations of traits with optimal values or when factors other than economics (e.g., ethical reasons) require certain restrictions on the selection programs.

The concept of discounted gene flow as a basis for derivation of economic weights was another milestone development that more correctly takes the number of expressions of the traits and the planning period into account (24). This approach was used in the development of a total merit index (TMI) for dairy bulls in Sweden during 1975, which included 12 traits: milk production, growth rate, female fertility, stillbirths, ease of milking, temperament, and six conformation traits (32). Development of TMI was made possible through integration of AI and milk-recording schemes.

Discussions in the last decade have often centered on economic values in limited market situations, e.g., milk quota or restrictions on herd size. Also, the use of customized indexes versus breeder-based indexes are frequently discussed because of their different target groups. Although such limitations or differences might be considered for short-term decisions at the farm level, national improvement programs should consider maximum gain in long-term net efficiency per animal. Although the choice of economic weights apparently is somewhat arbitrary, selection index results seem to be quite robust to at least moderate changes of economic weights (45).

Finally, increasing international exchange of genetic material has prompted the need to utilize global resources efficiently to maximize genetic gains. Such a scheme requires solid methods of animal comparisons on a global scale for a number of important traits. Substantial scientific effort has been, and is still being, placed on developing such methodology (1, 38). The International Bull Evaluation Service (INTERBULL) is actively involved in pertinent research, including both production and nonproduction traits and establishment of guidelines for international use of sire evaluations.

SURVEY OF PRESENT SELECTION INDEX APPLICATIONS IN DAIRY CATTLE

Within the framework of INTERBULL, surveys have been conducted at regular intervals on methods applied for sire evaluation and on traits considered in the selection schemes of major dairy countries in the world. Such surveys were performed during 1988 and 1992. The latter included 28 countries for production traits and 19 countries for beef and nonproduction traits, such as conformation, health, reproduction, and management traits (19, 20).

Twenty-five countries reported the use of BLUP procedures for evaluation of production traits (Table 1). A rapid change to the use of the animal model has apparently taken place in the last 4 yr. The advantages of simultaneous evaluation of cows and bulls and the improved possibilities to account for effects of nonrandom use of bulls, which is now much more the case in international breeding programs, certainly encouraged this change.

Specific selection indices for production traits, combining the yield of milk and its constituents into an economic index, are applied in 14 countries. All except two countries consider protein. Most countries give three to six times as much weight to protein as to fat. Some countries have switched completely to protein yield as the only selection criterion for production. Furthermore, a number of countries reported the use of a TMI including milk yield components without a separate composite index for production.

Application of TMI has been noted in an increasing number of countries. However, less than half the number of countries being sur-

TABLE 1. Genetic evaluation methods applied for production traits.

Evaluation method	Countries 1988	Countries 1992
	— (no.) —	
Contemporary comparison	5	3
BLUP		
Sire model	14	7
Sire-maternal grandsire model	4	3
Single-trait animal model	4	13
Multiple-trait animal model	0	2
Countries surveyed	27	28

veyed apply such a selection index. Table 2 shows that all of these countries include production and some conformation traits in their TMI. An additional three countries also include ease of milking, but only the Scandinavian countries also consider fertility, calving performance or stillbirth, and health traits in their TMI.

Lifetime profitability of dairy cows certainly involves a number of traits, the importance of which may vary by breed and environmental and economic conditions of production. Reviews by Burnside et al. (6) and Wynne-Jones (50) clearly pointed out that production during first lactation or product value is a good indicator of lifetime yield and longevity, but also that substantial space was left to consider other traits that contribute to lifetime productivity and profitability. Culling statistics of many dairy populations generally indicate that, after low production, fertility problems and mastitis are the two most common single causes of culling dairy cows. Furthermore, stillbirths occur in a number of breeds at the mean rate of 4 to 10% at first calving (25). Thus, it is surprising that so few countries have included into a TMI such functionally important traits as female fertility, stillbirth, or dystocia as a maternal trait, and resistance to mastitis, other than indirectly by udder and teat conformation.

The lack of interest in inclusion of these traits may have various causes. In some cases, sires are evaluated for these traits, but selection indexes have not been worked out. However,

in the majority of the cases no evaluations are available at all, which may be due to a lack of records or because recording and evaluation schemes are not integrated. Lack of interest may also be due to neglect of traits with low heritability without estimates of the real amount of additive genetic variation. Although mass selection is inefficient for such traits, modern AI programs based on integrated data of AI services, milk recording, and health recording offer other opportunities for effective selection.

Female Reproduction Traits

A number of subtraits contribute to variation in female fertility (e.g., chromosomal abnormalities, anatomical defects, rate of uterus involution, onset of normal cyclicity after parturition, signs of estrus, conception rate, and embryonic loss). Furthermore, the fertility of a virgin heifer, a first lactation cow, and an older cow must be looked upon as somewhat different traits (31).

Because of the complexity of the fertility traits and their interaction, it is extremely important that those traits be properly recorded in any breeding program of dairy cattle. Only then can different problems, such as various qualitatively inherited defects versus other quantitatively measurable traits, be differentiated.

Most of the commonly used measures of female fertility are based on nonreturn figures or number of AI services per female in combi-

TABLE 2. Traits considered in countries applying total merit index for dairy bulls.

Country	Production	Growth and beef characteristics	Conformation	Ease of milking	Temperament	Health	Fertility	Calving, stillbirth
Canada	x		x					
Denmark	x	x	x	x	x	x	x	x
Finland	x	x	x	x	x	x	x	x
France	x	x	x	x				
Germany	x		x	x				
Italy	x		x					
New Zealand	x		x	x				
Norway	x	x	x	x	x	x	x	x
Slovenia	x	x	x	x			x	x
Sweden	x	x	x		x	x	x	x
United Kingdom	x		x					
United States	x		x					

nation with an interval measure (for cows) such as days from calving to first AI. In less favorable recording situations, days open might be used.

In general, heritabilities estimated for these traits are low, ranging from .02 to .05. However, the additive genetic variation per se is large, as indicated by the coefficient of variation that is equal to or not much less than that for milk yield (18, 28, 31, 35, 40, 44, 48). The low heritabilities are explained by the large influence of environmental factors and also because fertility is recorded primarily as an all-or-none trait when based on the outcome of single inseminations.

A serious breeding concern is that estimates from a number of studies (21, 23) also present unfavorable genetic correlations, on average near .3, between various fertility measures and production. Thus, the functional and economic effects of inclusion versus neglect of female fertility in a long-term breeding program need to be considered.

An indication of these implications could be taken from the Swedish experience of combining fertility into the TMI of the Ayrshire type cattle with the trend experienced from the "holsteinization" of the Black and White cattle, where the TMI has been often set aside because of the consistent use of foreign sires of bulls. The genetic trends of bulls being progeny tested in different years are illustrated in Figure 1 (5). The trend for fertility for Swedish Red and White cattle is unchanged or slightly positive throughout this period despite a considerable improvement in production potential. The opposite trend is quite evident for the Black and White cattle, although both breeds produce at about the same level.

Calving Traits

Dystocia and stillbirths are certainly important correlated traits for first calvings, but a large proportion, 40 to 60%, of calves born dead do not result from difficult parturitions (25, 30). The expression of these traits reflects both maternal and calf effects and their interaction. Stillbirths are very simple to record objectively in any milk-recording scheme; however, calving performance is a subjectively scored trait that might require a special recording routine. Many countries provide informa-
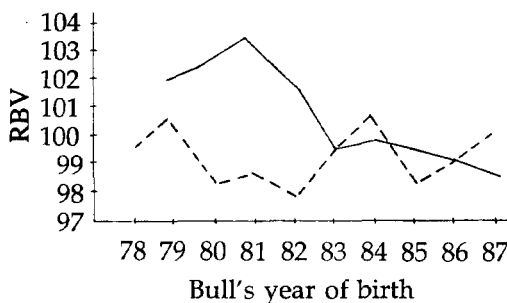

Figure 1. Trends in relative breeding values (RBV) of bulls for female fertility of the two major Swedish dairy breeds, Swedish Red and White (– – –) and Swedish Friesian (—), (5).

tion about calving performance as a calf (direct) trait to identify bulls that should not be mated to heifers. Fewer countries evaluate the dam trait, although this information would be better suited for long-term selection. Even fewer countries evaluate stillbirth, despite its simplicity to record.

Heritability estimates for stillbirth at first calving usually range from .02 to .04; calving difficulty, often reflecting the size of calf or pelvic conformation, usually has heritabilities from .05 to .10 (25, 30, 46, 47). Higher values have generally been obtained from threshold models compared with those from linear model analyses. Despite the low heritability, stillbirth rates vary considerably among progeny groups, up to 20% stillborn calves in large groups of first-calvers, both as a dam trait and as a calf trait in the Black and White cattle in Sweden.

Udder Health Problems

Mastitis, both clinical and subclinical, is by far the most costly infectious disease of dairy cows. Appropriately recorded clinical cases of mastitis show heritabilities approximately .02 to .05 (34, 42, 49). Lyons et al. (23) reported somewhat higher values. As in the case of reproductive traits, the genetic variation of this categorically recorded trait is considerable. As an indicator of both clinical and subclinical mastitis, SCC shows higher heritability (.05 to .15) and reasonably high genetic correlations with clinical cases of mastitis (.6 to .8). The SCC offers easily measured values of udder health for selection purposes as early as the

first lactation (2, 9, 49). Antagonistic genetic correlations of production and resistance to mastitis of the order .3 seem to exist and necessitate the consideration of both traits in long-term selection. Udder and teat conformation can be used partially for indirect selection for improved udder health (36, 39). However, a large proportion of the genetic variation in resistance to mastitis is not related to conformation traits.

The use of SCC for selection purposes has been widely discussed because the elevation of SCC with an infection is a clear indication of the occurrence of infection as well as of the immunological response to combat the infection. Recent studies clearly indicate, however, that the genetic correlation with clinical cases of mastitis is reasonably high and that the relationship is linear (33). Low SCC follow low prevalence of mastitis, and high SCC indicate high prevalence. Thus, the validity of using SCC as an indirect measure to improve mastitis resistance has been strengthened.

Recent Danish and Swedish studies reveal large differences among Holstein bulls for breeding values of mastitis resistance (5, 37). The "holsteinization" of the Black and White cows in Sweden has, on average, led to a marked increase in production without a change in the prevalence of mastitis, despite the generally observed antagonistic relationship (33). A possible deterioration has probably been counteracted by correlated positive effects of simultaneously improved udder conformation. However, serious exceptions are available that definitely call for direct consideration of mastitis traits into the selection scheme.

EFFICIENCY OF INDEX SELECTION FOR TOTAL MERIT

To investigate the importance of inclusion of traits relating to reproduction and udder health into a TMI in combination with production, several alternatives for construction of selection indexes were examined. Thus, a simplified breeding objective, consisting of protein yield, female fertility, and clinical mastitis, was defined that included three important components contributing to lifetime productivity of dairy cows. These three traits were assumed to be recorded routinely in an integrated record-ing scheme for milk, AI, and health. Information on SCC and udder conformation was used in addition to the breeding goal traits. Genetic and phenotypic parameters were chosen from the literature and are given in Table 3. The economic weights were chosen in close agreement with those of Christensen (7) for Danish conditions and of Rogers (36) for North American conditions. Two alternative sets of weights were chosen and are expressed in relative units per genetic standard deviation in Table 4. Three alternative recording and testing schemes considered are shown in Table 5. Effects of progeny testing bulls were analyzed based on 50, 100, and 150 daughters. The first alternative assumed recording of only production, although the breeding objective still included fertility and mastitis resistance. The second alternative used information on all traits, but no information on mastitis or SCC was available in alternative 3. A separate alternative included all information, but index weights were derived with a restriction resulting in unchanged mastitis rate and fertility.

The accuracy of the TMI for each alternative of bull testing was calculated. Because the selection response for each selection path is proportional to the accuracy of estimating the breeding value in relation to the aggregate genotype, the different accuracies of the TMI were taken as plausible measures of response, without any further specification of the population structure or selection procedure. However, to visualize the amount of genetic change that the different schemes might give because of the bull selection, it was assumed that an average selection differential of one standard deviation unit was practiced for one round of selection among bulls.

RESULTS

Results in Table 6 show that realistic weighting of production, mastitis, and fertility implies that a considerable loss in bull selection accuracy, 15 to 25%, follows single-trait selection for production versus consideration of all three categories of traits into an index. Because of unfavorable correlations with production, mastitis resistance and fertility should gradually decline if selection is based on production only. Inclusion of udder conformation has only marginal effects.

TABLE 3. Assumed heritabilities (boldface diagonal), genetic correlations (above diagonal), and phenotypic correlations (below diagonal).

Trait	Protein	Mastitis	Fertility	SCC	Udder conformation
Protein	**.25**	.30	-.30	.30	-.20
Mastitis	-.10	**.03**	0	.70	-.30
Fertility	-.20	0	**.04**	0	0
SCC	-.10	.10	0	**.10**	-.30
Udder conformation	-.10	-.10	0	-.10	**.20**

The advantage of increased group size of daughters is clearly demonstrated when traits with low heritability are included. Increased accuracy in evaluation of production only, through increased daughter groups, has limited value compared with recording and inclusion of fertility and mastitis into a TMI. The restricted index showed that the unfavorable, correlated responses in fertility and mastitis from bull selection for production could be offset at the expense of 12 to 15% lowered gain in production when no other assumptions for selection are changed.

FUTURE CONSIDERATIONS

The presented surveys and examples of alternative recording schemes and selection indexes imply that more future research should be on methods for recording and evaluating, economically and genetically, traits other than production. More economic gain could be obtained by controlling unfavorable correlated responses for reproduction and udder health, thereby keeping costs low for culling from mastitis and fertility problems, which would suggest the need for more integrated recording schemes in many countries to accomplish this goal.

Accurate selection for a TMI, as described, requires more research to obtain reliable estimates of genetic and phenotypic parameters applicable to the trait recording schemes and data obtained for each population or country. The same applies to estimation of economic weights.

The development of genome mapping and the detection of possible markers or major genes for economically important traits will most likely add new dimensions to future evaluations of bulls. The use of marker-assisted selection in progeny-testing schemes, and especially in nucleus breeding plans, has the potential to increase selection response for important traits. As DNA technologies and statistical methods are improved, the costs of such systems are reduced, and the utilization of markers can be expected to become economically justified (4). Furthermore, direct and early selection at the DNA level for elimination of defects, for example bovine leukocyte adhesion deficiency, might be very effective. However, selection for individual genes or markers also calls for evaluation and monitoring of all important production and functional traits because of possible risks of unfavorably correlated responses.

TABLE 4. Means, genetic standard deviations, and economic weights of traits included in the breeding objective under two alternatives, A and B.

Trait	Mean	Genetic standard deviation	Economic weight per genetic standard deviation	
			A	B
Protein, kg	230	16	2.5	3.5
Mastitis, %	30	10	-1	-1
Fertility, % NR[1]	67	9	1.5	1.5

[1]Nonreturn.

TABLE 5. Alternative constructions for a selection index.

Economic weights	Testing alternative[1]	Recorded traits on daughters for progeny testing of bulls
Alternative A	1 a, b, c	Protein
	2 a, b, c	Protein, mastitis, fertility, SCC, and udder[2]
	3 a, b, c	Protein and udder[2]
Alternative B	1, 2	As above
Restricted	a, b, c	As alternative 2 but restriction for unchanged mastitis and fertility

[1]Daughters: a = 50, b = 100, and c =150.

[2]Fifty daughters evaluated in all altenatives.

The most important international development would be the availability of breeding values for bulls for all the most economically important traits. The weighting of traits, and thus the construction of TMI, then would be a matter for each country to decide, depending on the variable conditions of economic markets. Globalized programs for dairy cattle breeding would benefit from better acceptance of TMI in each country. In addition, international publication of genetic evaluations enables somewhat different weighting of traits when the bulls are selected for use in different countries. Furthermore, the present potential of heavy international use of individual bulls definitely requires accurate proofs for a range of economically or functionally important traits to prevent the spread of defects or other undesirable genes.

TABLE 6. Accuracy (R_{TI}) of total merit index (TMI) and responses from one round of bull selection in breeding objective traits for alternative index constructions.

Alternative economic weights and testing scheme	R_{TI}	Response[1]		
		Protein	Mastitis	Fertility
		(kg)	(%)	(% NR)[2]
A1a (Protein)	.640	14.0	2.6	-2.4
b	.681	14.9	2.8	-2.5
c	.696	15.3	2.9	-2.6
2a (All traits)	.737	12.1	1.4	.1
b	.819	12.3	.9	.8
c	.859	12.3	.6	1.2
3a (Protein and	.641	14.0	2.5	-2.4
b udder)	.683	14.9	2.6	-2.5
c	.699	15.2	2.7	-2.6
B1a (Protein)	.753	14.0	2.6	-2.4
c	.819	15.3	2.9	-2.6
2a (All traits)	.801	13.2	2.1	-.7
c	.901	13.8	1.5	0
Restricted				
a (All traits)	.693	11.1	0	0
b	.816	12.4	0	0
c	.870	13.0	0	0

[1]Per generation with standardized selection differential = 1.

[2]Percentage of nonreturn.

CONCLUSIONS

The international survey of the present use of TMI for dairy cattle clearly showed much room for improvement. A serious constraint to overcome the present deficiencies seems to be the lack of recording systems or ways to organize records of pertinent traits. Integrated computer systems should be developed in many more countries to handle data from milk-recording, AI, and possibly also from health-recording schemes to establish comprehensive data banks for each cow, for herd management, and for information for multiple-trait genetic evaluation of bulls.

Thus, the basic proposal of Hazel (12) from 50 yr ago is still valid, at least for future applications for dairy cattle. The combination of production, reproduction, and health traits according to basic principles of selection index has been very well accepted in the Scandinavian countries and is certainly supported by results of this study, as well as a number of recent research results from other parts of the world. Further developments in computer and statistical evaluation techniques and in molecular genetics and reproductive technologies most likely will enhance future possibilities for efficient selection. Nonetheless, correct definitions of the real breeding objectives, availability of relevant records, and the application of properly constructed indexes for selection will determine actual progress.

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