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Invited review: The future of selection decisions and breeding programs: What are we breeding for, and who decides?

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ABSTRACT

Genetic selection has been a very successful tool for the long-term improvement of livestock populations, and the rapid adoption of genomic selection over the last decade has doubled the rate of gain in some populations. Breeding programs seek to identify genetically superior parents of the next generation, typically as a function of an index that combines information about many economically important traits into a single number. In the United States, the data that drive this system are collected through the national dairy herd improvement program that began more than a century ago. The resulting information about animal performance, pedigree, and genotype is used to compute genomic evaluations for comparing and ranking animals for selection. However, the full expression of genetic potential requires that animals are placed in environments that can support such performance. The Agricultural Research Service of the US Department of Agriculture and the Council on Dairy Cattle Breeding collaborate to deliver state-of-the-art genomic evaluations to the dairy industry. Today, most breeding stock are selected and marketed using the net merit dollars (NM$) selection index, which evolved from 2 traits in 1926 (milk and fat yield) to a combination of 36 individual traits following the last NM$ update in 2018. Updates to NM$ require the estimation of many different values, and it can be difficult to achieve consensus from stakeholders on what should be added to, or removed from, the index at each review, and how those traits should be weighted. Over time, the majority of the emphasis in the index has shifted from yield traits to fertility, health, and fitness traits. Phenotypes for some of these new traits are difficult or expensive to measure, or require changes to on-farm habits that have not been widely adopted. This is driving interest in sensor-based systems that provide continuous measurements of the farm environment, individual animal performance, and detailed milk composition. There is also a need to capture more detailed data about the environment in which animals perform, including information about feeding, housing, milking systems, and infectious and parasitic load. However, many challenges accompany these new technologies, including a lack of standardization or validation, need for high-speed internet connections, increased computational requirements, and interpretations that are often not backed by direct observations of biological phenomena. This work will describe how US selection objectives are developed, as well as discuss opportunities and challenges associated with new technologies for measuring and recording animal performance.
Key words: breeding programs, genetic improvement, selection objectives, total merit indices

INTRODUCTION

Selection indices are essential tools in modern dairy cattle breeding because they enable information about many traits to be combined into a single value for ranking animals and making selection decisions. The ideal breeding objective for dairy cattle remains a popular topic, even if consensus is elusive, and is frequently discussed in the scientific and popular literature (e.g., Hazel et al., 1994; Philipsson et al., 1994; VanRaden, 2004; Miglior et al., 2005; Shook, 2006; Miglior et al., 2017; Cole and VanRaden, 2018; Binversie, 2019; Dechow, 2020; Schmidt, 2020). There is no single selection objective that is ideal for all populations, or all herds within a population, but there is a general set of principles that should be followed when developing an index (e.g., Cameron, 1997).

Historically, selection indices in the United States were developed by the United States Department of Agriculture (**USDA**) and by purebred dairy cattle

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associations (**PDCA**). Input has also been provided by scientists at land-grant universities and technical experts at breeding companies, using data available through the national milk recording system and breed type appraisal programs. Proposed indices from the USDA were typically reviewed by groups of experts, and information about the derivation of the indices was published in technical and trade publications, ensuring confidence in the values because of that review process. Recently, genetic evaluations for novel traits and new selection indices have been computed and distributed by companies such as GENEX and Zoetis. Both of these organizations publish their own indices, which include a combination of traits from the Council on Dairy Cattle Breeding (**CDCB**) evaluations and their own proprietary traits (i.e., hoof health in the case of GENEX, and cow and calf health traits in the case of Zoetis). This provides farmers with new tools and may drive demand for new phenotypes, but transparent review processes are often lacking. Correlations among indices are generally strong (T. J. Lawlor Jr., Holstein Association USA, Brattleboro, VT; personal communication), and in such cases, it is unclear if new tools provide new information or serve only as marketing tools.

This paper will describe how decisions about selection indices are made in the United States, discuss traits that may be included in future changes to existing indices, and identify opportunities associated with new technologies for recording animal performance. Although the focus is on the US dairy sector, examples from other countries are discussed when appropriate.

DEVELOPMENT OF SELECTION OBJECTIVES

Who Are the Participants in the US Dairy Sector?

To explain how selection decisions are made, we must briefly review the stakeholders in the process (Wiggans et al., 2017; Figure 1). The Animal Genomics and Improvement Laboratory is part of the Agricultural Research Service, USDA's in-house research arm, and was responsible for the development of the indices shown in Table 1 (sometimes under other laboratory names due to Agricultural Research Service organizational changes). The CDCB operates the national genetic evaluation system and maintains the national cooperator database. The CDCB board includes representatives from all key industry participants, including the National Dairy Herd Information Association (**NDHIA**), Dairy Records Processing Centers, the National Association of Animal Breeders, and the PDCA. The field service organizations and milk testing laboratories that operate the national milk recording program are represented by NDHIA; the organizations that aggregate and distribute milk testing data and provide herd management information are represented by the Dairy Records Processing Centers; the AI companies, who own most of the bulls and many elite females, are represented by the National Association of Animal Breeders; and the breeders, who own most of the elite cattle, are represented by the PDCA. In addition, CDCB has several advisory groups that include farmers, researchers, and allied industry personnel that review and provide feedback on data quality and proposed changes to the genetic evaluation system. Scientists from the land-grant universities provide valuable technical expertise to the Animal Genomics and Improvement Laboratory and CDCB, both as individual consultants and through the SCC-084 Multistate Research Coordinating Committee and Information Exchange Group. This group meets annually to share results and plan future research on selection and mating strategies to improve dairy cattle performance, efficiency, and longevity. All of these participants in the national dairy improvement program have opportunities to influence the selection indices adopted by CDCB, some directly, and others indirectly.

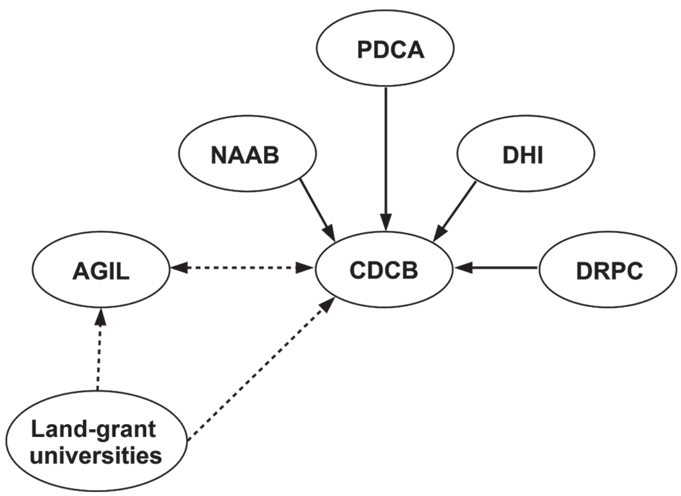

Figure 1. The general structure of the US dairy cattle improvement sector. Solid lines indicate board membership in an organization, and broken (dashed) lines represent advisory relationships. AGIL = Animal Genomics and Improvement Laboratory, Agricultural Research Service, United States Department of Agriculture (constructs the index); CDCB = Council on Dairy Cattle Breeding (operates the national genetic evaluation system and maintains the national cooperator database); DRPC = Dairy Records Processing Centers (aggregate and distribute milk testing data and provide herd management information); NAAB = National Association of Animal Breeders (represents breeding companies); DHI = Dairy Herd Improvement (oversees the national milk recording program); PDCA = Purebred Dairy Cattle Associations (represents breeders). Scientists at the land-grant universities provide technical expertise.

In addition to the organizations with direct representation on the CDCB board, there are several entities that participate in the collection and transfer of genomic information (Figure 2). The genomic nominators are responsible for collecting DNA samples from the animal owner, providing CDCB with information about the animals sampled, and transferring the DNA samples to the genotyping laboratory. The genotyping laboratory extracts DNA from samples, prepares SNP genotypes, provides summary information back to the nominator, and transfers the genotypes to the CDCB. Genomic evaluations are sent from the CDCB to the nominators, and on to the records providers. Both the nominators and laboratories must meet quality certification guidelines before they are permitted to participate in the system, and their performance is audited on an annual basis.

How Are Decisions About Selection Criteria Made?

How Are the Index Weights Determined? Selection indices must be periodically updated to include new traits and reflect changing economic conditions, as well as changing genetic parameters between and among traits. From the development of the first USDA index (Norman and Dickinson, 1971) until the present (VanRaden et al., 2018), a collaborative model has been used to propose and adopt changes to the indices. Although an argument can be made that changes should be driven strictly by mathematics—and we are sympathetic to this position—the reality is that tools will not be adopted unless the intended users perceive value in the tool. The net merit dollars (**NM$**) weights are primarily based on selection index theory, with fine-tuning based on consensus expert opinion, which reflects the well-known challenge of computing index weights (Freeman, 1984). It is also more difficult to compute the incomes and expenses associated with traits in the index than the textbooks suggest, and input from the field is very helpful in that regard. Our experience over the last 50 yr suggests that collaboration not only drives increased adoption of the indices, it also builds support for other communal efforts, such as the recording of new phenotypes so that they may eventually be included in the index.

Who Owns the Index? Responsibility for the national cooperators database and the genetic evaluation system was passed from USDA to CDCB in 2013, but NM$ and its companion indices (cheese merit, fluid merit, and grazing merit; VanRaden, 2000; Gay et al., 2014) require both index weights and genetic values to compute. When an index is owned by a PDCA or an AI company, it is clear who has the authority to make changes and the responsibility for distributing the calculations. In the case of NM$, USDA and CDCB share these roles: USDA is responsible for construction of the index, and CDCB provides the data needed to calculate and distribute the values. Both organizations

Table 1. Traits included in United States Department of Agriculture selection indices[1] and the relative emphasis placed on each, 1971–2018 (Cole and VanRaden, 2018)

	Relative emphasis on trait (%)										
Trait[2]	PD$ (1971)	MFP$ (1976)	CY$ (1984)	NM$ (1994)	NM$ (2000)	NM$ (2003)	NM$ (2006)	NM$ (2010)	NM$ (2014)	NM$ (2017)	NM$ (2018)
Milk	52	27	−2	6	5	0	0	0	−1	−1	−1
Fat	48	46	45	25	21	22	23	19	22	24	27
Protein	—	27	53	43	36	33	23	16	20	18	17
PL	—	—	—	20	14	11	17	22	19	13	12
SCS	—	—	—	−6	−9	−9	−9	−10	−7	−7	−4
UC	—	—	—	—	7	7	6	7	8	7	7
FLC	—	—	—	—	4	4	3	4	3	3	3
BWC	—	—	—	—	−4	−3	−4	−6	−5	−6	−5
DPR	—	—	—	—	—	7	9	11	7	7	7
SCE	—	—	—	—	—	−2	—	—	—	—	—
DCE	—	—	—	—	—	−2	—	—	—	—	—
CA$	—	—	—	—	—	—	6	5	5	5	5
HCR	—	—	—	—	—	—	—	—	1	1	1
CCR	—	—	—	—	—	—	—	—	2	2	2
LIV	—	—	—	—	—	—	—	—	—	7	7
HTH$	—	—	—	—	—	—	—	—	—	—	2

[1]PD$ = Predicted Difference Dollars (Dickinson et al., 1971); MFP$ = Milk-Fat-Protein Dollars (Norman et al., 2010); CY$ = Cheese Yield Dollars (Norman, 1986); NM$ = Lifetime Net Merit Dollars (VanRaden and Wiggans, 1995).

[2]PL = productive life; UC = udder composite; FLC = feet and legs composite; BWC = body weight composite; DPR = daughter pregnancy rate; SCE = sire (direct) calving ease; DCE = daughter (maternal) calving ease; CA$ = calving ability dollars; HCR = heifer conception rate; CCR = cow conception rate; LIV = cow livability; HTH$ = health dollars.

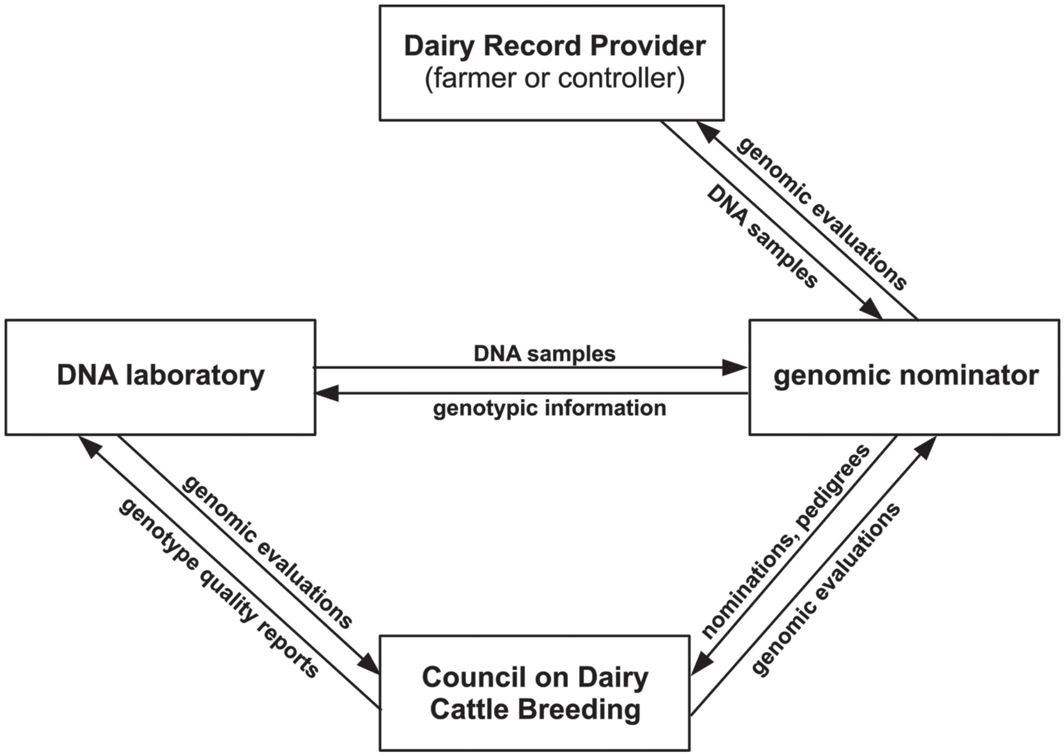

Figure 2. Flow of information among participants in the national genomic evaluation system.

have input into the evolution of the index, but neither owns it. Lifetime net merit was initially developed by USDA scientists (VanRaden and Wiggans, 1995), but it has remained relevant because of the USDA-CDCB partnership. The success of NM$ has not prevented other organizations from developing their own selection tools, and farmers have many indices from which to choose if NM$ does not meet their expectations.

How Do We Validate Our Indices? Selection indices are constructed using many calculations based on a substantial body of scientific theory (e.g., Hazel et al., 1994). Complex traits, such as longevity, remain difficult to model properly, and there is some disparity between management practices in the field and optimal economic strategies (Schmitt et al., 2019; De Vries, 2020). It can be difficult to confirm that realized selection gains are consistent with index predictions, but some recent reports show that animals with greater genetic merit are more profitable than their contemporaries with lower rankings. In the United States, scientists from Zoetis and the University of Pennsylvania recently showed that cows in the top quartile for the Dairy Wellness Profit index had greater lifetime profit than herdmates in lower quartiles (Fessenden et al., 2020). The lack of farm-level income and expense data in the national cooperator database makes it difficult to perform routine validation of the index, but collaboration with projects such as the Dairy Profit Monitor program at Cornell University (https://cals.cornell.edu/pro-dairy/our-expertise/business/dairy-profit-monitor) could support such an effort.

How Have Selection Indices Evolved Over Time?

What Traits Are in the Index? The emphasis placed on each trait in each revision of the selection index is shown in Table 1, and the rate at which new traits are added to the index has increased considerably in recent years. This represents changes in dairy economics, an improved understanding of the biology of the cow, and greater ease of collecting and transferring data. The first selection index published by USDA was the Predicted Difference Dollars index, which included information about milk and fat production (Norman and Dickinson, 1971). Although it was recognized at the time that other traits might have economic importance, milk and fat were the only traits with enough phenotypic information available to support genetic evaluations. Protein yield was added to Predicted Difference Dollars in 1976 to produce the Milk-Fat-Protein Dollars index (Norman et al., 1979), and an index for cheese yield was developed in 1984 (Norman, 1986).

This was the status quo until 1994, when productive life and SCS were combined with the yield traits to produce the first iteration of the Lifetime Net Merit index (VanRaden and Wiggans, 1995).

Although the combination of fitness, conformation, and production traits included in the first version of NM$ in 1994 set it apart from most of its international competitors, the Scandinavian countries began recording health and fertility data in the 1960s and computing genetic evaluations for those traits in the 1970s (Philipsson and Lindhé, 2003). Their experience showed that selection objectives that include traits with low heritabilities can produce worthwhile gains in cow health and fertility. Leitch (1994) reviewed 19 contemporary selection indices and found that only 2 (Danish S-Index and US NM$) included mastitis resistance, 1 included fertility (Danish S-Index), and 1 included productive life (US NM$). In a review based on an independent survey, Philipsson et al. (1994) identified several other countries' indices (Finland, Norway, Slovenia, and Sweden) that also included fitness traits. When Miglior et al. (2005) revisited the subject a decade later, each of the 17 indices reviewed included 1 or more fitness traits as part of the selection criterion. This trend toward the inclusion of more fitness traits in total merit indices has continued (Cole and VanRaden, 2018), and it is now more remarkable when an index does not include such traits than when it does.

There Is No Universal Standard. It is tempting to assume that it is possible to define a universal total merit index, but that is not possible because every farmer operates in a slightly different economic and environmental setting than their neighbors. In theory, every farm should actually use its own selection index that is customized to its financial situation and business objectives (Gjedrem, 1972). In practice, farms with similar operating and financial characteristics can use the same index with little loss of efficiency. It is also difficult to assign direct economic values to some traits, most notably conformation traits. Different breeders have different goals, which can affect their breeding programs. A commercial dairy that derives its income principally from the sale of milk solids will have different incomes and expenses than a seedstock breeder who also sells embryos and elite germplasm, and they may benefit from using different indices. Lifetime net merit is explicitly developed for use by commercial dairy farmers (VanRaden, 2004), and Holstein Association USA's Total Performance Index is intended for use by registered cattle breeders who often sell genetics as well as milk.

More than 1 index is needed because farmers sell their products into different markets (e.g., VanRaden, 2000), have different personal preferences (e.g., Martin-Collado et al., 2015), and strategies for maximizing profit vary (e.g., Berry et al., 2019). As noted earlier, the CDCB publishes 4 separate indices (lifetime net merit, fluid merit, cheese merit, and grazing merit) to provide farmers with options that best match their needs. The strategy of providing multiple indices to its farmers is certainly not unique to the United States For example, when the Australian Dairy Herd Improvement Scheme (now DataGene) revised the Australian Profit Ranking index in 2016, they replaced it with 3 new indices (Byrne et al., 2016). The Balanced Performance Index, Health Weighted Index, and Type Weighted Index allow their farmers to focus on trait groups that are most important to them within a technically sound framework.

Are There Too Many Indices Already? The last several years have seen the development of many new selection indices marketed to commercial dairy farmers. In contrast to NM$ and indices published by PDCA, many of these new indices are promoted by breeding companies as a means of differentiating their products. Several selection indices currently available to US dairy farmers are shown in Table 2, although this is not an exhaustive list (some organizations do not make the details of their index publicly available). These tools include indices developed by USDA, PDCA (e.g., American Jersey Cattle Association), and commercial organizations (e.g., Zoetis). In general, most indices are similar in that they are seeking to find a balance between productivity (the direct source of much farm income) and fitness traits (often a source of direct costs). Direct comparisons are challenging because some indices are available only for bulls marketed by the publisher of the index. Most differences among indices are due to the inclusion of different sets of traits, or to the differential weighting of such traits in the index. Some companies develop proprietary evaluations to differentiate their offerings from those of their competitors. Correlations among these indices generally are very strong, and there is minimal reranking of bulls when moving from one index to another (T. J. Lawlor Jr., Holstein Association USA, Brattleboro, VT; personal communication). However, farmers may not be able to clearly describe differences between each index, providing some opportunities for confusion. There also is concern that marketers may be over-stating the importance of the differences between the indices.

Are Selection Indices Responsible for Reducing Diversity in Some Breeds? It is tempting to place the blame for the ongoing loss of genetic diversity in US Holsteins (e.g., Maltecca et al., 2020) on breeders who avidly pursue high-index animals, but

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