A 100-Year Review: Identification and genetic selection of economically important traits in dairy cattle[1]

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ABSTRACT

Over the past 100 yr, the range of traits considered for genetic selection in dairy cattle populations has progressed to meet the demands of both industry and society. At the turn of the 20th century, dairy farmers were interested in increasing milk production; however, a systematic strategy for selection was not available. Organized milk performance recording took shape, followed quickly by conformation scoring. Methodological advances in both genetic theory and statistics around the middle of the century, together with technological innovations in computing, paved the way for powerful multitrait analyses. As more sophisticated analytical techniques for traits were developed and incorporated into selection programs, production began to increase rapidly, and the wheels of genetic progress began to turn. By the end of the century, the focus of selection had moved away from being purely production oriented toward a more balanced breeding goal. This shift occurred partly due to increasing health and fertility issues and partly due to societal pressure and welfare concerns. Traits encompassing longevity, fertility, calving, health, and workability have now been integrated into selection indices. Current research focuses on fitness, health, welfare, milk quality, and environmental sustainability, underlying the concentrated emphasis on a more comprehensive breeding goal. In the future, on-farm sensors, data loggers, precision measurement techniques, and other technological aids will provide even more data for use in selection, and the difficulty will lie not in measuring phenotypes but rather in choosing which traits to select for.
Key words: selection goal, production trait, functional trait, novel trait

INTRODUCTION

Genetic selection for important traits has helped transform and advance the dairy cattle industry. Specific traits considered for selection in dairy cattle populations have evolved with time as a response to changes to the needs of producers, consumers, and society with the aid of advances in technology and trait recording programs.

As outlined by Shook (1989), a potential trait must meet several criteria before it can be considered for selection in dairy cattle populations. First, either it should have an economic value as a marketable commodity or its improvement should reduce production costs. Second, the trait must have sufficiently large genetic variation and heritability. Third, the trait should be clearly defined, measurable at a low cost, and consistently recorded. Finally, an indicator trait may be favored if it has a high genetic correlation with the economically important trait, reduces recording costs, has a higher heritability, or can be measured earlier in life.

The economic value of traits has historically been the driver for genetic selection. From the 1930s to the 1970s, the focus of selection was solely on increasing milk production. Despite some early concern over selecting exclusively for yield, which was expected to cause a corollary decline in overall fitness, the industry strove to achieve maximum genetic change in the most financially lucrative area, which was production. The need to identify and select for additional traits emerged mainly from the recognition of the correlated genetic decline in other important traits. Many countries have shifted toward more balanced selection objectives by including more weight on previously undervalued nonyield traits (Miglior et al., 2005).

The second criterion concerns genetic variation and heritability of a trait, which are central to the rate of genetic progress possible within a selection program. Traits vary in the amount of phenotypic and genetic variation observed, and they may be more or less heritable. Traits may also be contingent on one another,

with correlations either positive or negative and genetic and phenotypic correlations either strong or weak. Such correlations may be exploited by the use of indicator traits, which may be favored if they are more readily available than a trait of interest.

A major boon for the progression of genetic selection has been the recording and access to clearly defined, accurate, and cost-effective phenotypes. The continuous increase in data collected throughout the production chain has brought forth many opportunities and a large number of traits with genetic evaluations for consideration. However, this has also resulted in a large number of potential traits to be considered for inclusion in selection programs and ultimately balanced appropriately. Careless selection, changing selection goals, or having many different objectives can reduce selection pressure (Meadows, 1968) and can have an undesirable permanent effect on the population.

The conception, development, and application of multitrait index selection has played a pivotal role in successful and progressive selection in many countries. By weighting each trait according to its independent effect on net profit and using genetic and phenotypic parameters to weight traits measured in individuals and relatives, the correlation of index with genetic variation in net profit can be maximized (Hazel, 1943; Hazel et al., 1994). Traits considered in selection vary between countries because of differences in milk and component prices, costs of inputs and services, production environments, and availability of phenotypes. These factors can frequently change, and modifications need to be considered and researched continually. The identification of traits that are presently important for genetic selection and those that will be essential in the future is a vital aspect of selection research.

Milk recording began in North America in 1905 and thus provided the foundation for selection on milk production. Cattle shows at county fairs made conformation traits very popular as well. Technological advances, in particular the advent of AI in the late 1930s, created a division between producers who wanted cows to produce milk and those who wanted good-looking cows that produced milk. Artificial insemination organizations aimed their bull selection programs toward both types of producers. Gradually, producers recognized that fat and protein yields and longevity were also important to keeping the costs of production within reason. Behavior and health traits were incorporated soon afterward, demonstrating an increased awareness of the economic importance of these traits but also representing increasing societal concerns with intense production systems.

The rapid developments in genomic information, automated data recording technologies, and modern analytical techniques over the past decade are setting the stage for a new era in dairy cattle breeding. Here we review the development of phenotypes used in dairy cattle selection over the past century (see Appendix Table A1).

PRODUCTION

A century ago, selection in dairy cattle focused on high milk and fat production. In the late 1800s and into the 1900s, many breed associations, in addition to their standard herd register, worked to promote better dairy cows by recording cow merit through milk recording for the inclusion of cattle in advanced registries (Becker and McGilliard, 1929). These registries went by various names, including Advanced Registry for Ayrshire, Register of Production for Brown Swiss, Advanced Register for Guernsey and Holstein, and Register of Merit for Jersey. The Babcock test, invented and made public in 1890 by S. M. Babcock, provided an accurate and easy method for the determination of milk fat content in milk testing. The testing of a large number of purebred cows through milk testing programs and the organization of records into published volumes of the Advanced Register and Register of Merit provided the foundation for locating high-producing blood lines and the study of the inheritance of milk and fat production (Fohrman, 1926). Meade (1921) evaluated the performance of Guernsey sires and their transmitting ability and concluded that the best method for selection may be to consider the percentage production of all advanced registry daughters based on standardized requirements according to age. The male line received the greatest attention in selection because the sire's heredity was most accurately indicated by his daughters' production, more so than the dam based on her own production record (Graves, 1925). A recognized fault of production records in an advanced registry for selection purposes was that records included only daughters that were put on test and met advanced registry standards. Later, some breed organizations initiated a further herd test or herd-improvement registry where dairy producers were required to test and report production of all cows in their herd. Using the descendants of 2 cows disparate for their fat tests, Burrington and White (1925) demonstrated that the difference in test could be maintained over generations. Copeland (1927) expressed that dairy cattle breeders had thus far concerned themselves chiefly with increasing milk yield traits and concluded that more improvement in total fat production could be accomplished by selecting for high fat percentage along with milk yield.

Traits also considered by breeders to aid in the selection of animals to improve production were body

conformation traits. The thought was based on the view that conformation of the cow shows her probable production and that the conformation of the sire will be transmitted to his daughters, implying their probable production (Gowen, 1926). Gowen (1920) attempted to study conformation and its relation to milk-producing capacity through the calculation of phenotypic correlations. He confirmed the existence of the relationship between body conformation and production that was common belief among producers, although he concluded that conformation was a poor guide for milk production. Body weight and other measurements indicating size and shape were related to milk production (but not fat percentage) and were inferior to production records of ancestors for breeding for milk production (Gowen, 1926). Consideration of conformation traits remained in the forefront for breeders because an easily measured indicator for production was in demand. The true value of conformation in breeding for production was unclear, though, and Copeland (1941) reported only a slight relationship. Tyler and Hyatt (1948) found an intraherd relationship of 0.19 between conformation and average fat record and stated that selecting within a herd for conformation would not substantially improve fat production. Harvey and Lush (1952) found a genetic correlation of 0.18 between conformation and fat production from daughter–dam pairs. O'Bleness et al. (1960) studied the genetic correlations between production traits and individual conformation traits, the strongest of which were fat with pin bone width (0.39–0.40), rear udder shape (−0.54), and fore teat length (0.42) and with milk, dairy character (0.95–0.98). However, with an index, selection on the basis of milk production alone would be almost as effective as including conformation traits as well.

More measures of producing ability related to the lactation curve and persistency began to appear. The 2 main factors in total yearly milk and fat production were the yield during the maximum month and the persistency of production or the rate of decline (Turner, 1926). Turner (1926) suggested inheritance of fat production during the month of maximum production and endorsed consideration of persistency in selecting breeding animals. Copeland (1937) studied Herd Improvement Registry records of the American Jersey Cattle Club, discovered that some cows maintained their production longer than other cows under similar conditions, and ruled that lactation persistency was an inherited trait.

Gaines and Overman (1938) discussed the American Dairy Cattle Club's step toward requiring estimates of milk protein yield on the advice of the club's geneticist that protein was the most biologically valuable milk component. However, at the time no practical field test for protein existed. The importance of the nonfat component of milk, or SNF, increased due to the awareness of the nutritional value of SNF and its effect on milk processing. Data presented by Richardson and Folger (1950) suggested that SNF contents were inherited and that its relationship with fat was nonlinear. Around the 1950s, changes to the milk pricing structure were proposed to better reflect the importance of, and compensate producers for, both fat and SNF contents in milk. With an economic value projected for SNF, dairy cattle breeders would seek to improve contents in their cows. The heritability presented by Johnson (1957) for SNF was 0.34 for both Holstein and Jersey breeds. This study also reported very strong genetic correlations between different milk components, deducing that selection for one would equate to selecting for the others but with less pressure. Nonfat components were expensive and difficult to obtain for large numbers of cows, thus limiting the number of observations for this trait. Legates (1960) and Laben (1963) reviewed the many factors affecting SNF. Selection at the time emphasized total milk yield per cow, which returned the greatest value for milk, but farmers were encouraged to test for SNF to help build knowledge of its variation and possible future economic gains (Laben, 1963). The cost of testing milk for protein was an added expense that could potentially be avoided, as protein still increased by selecting for correlated fat and milk yields (Van Vleck, 1978).

Infrared methods for the analysis of milk samples for fat, protein, and lactose content delivered more rapid and less expensive measures than those previously available (Biggs, 1967). Protein testing became much more commonplace in the 1970s using this technology and became standard in milk testing. Milk processors began paying premiums for protein, and the number of cows with a higher genetic propensity to produce protein increased rapidly as protein was added into national selection indices (Shook, 2006). A shift toward increased emphasis on protein yield in selection indices occurred in many countries.

Although total protein content in milk was the primary consideration for selection, genetic variability and milk protein variants garnered additional attention. Aschaffenburg and Drewry (1955) first reported a genetic polymorphism of β-LG producing 2 different forms. Genetic variation was next reported in α-LA (Blumberg and Tombs, 1958) and in the CN (Aschaffenburg, 1961). The effects of the many discovered milk protein variants were considered important to achieving specific requirements for the dairy industry, including cheese manufacturing. Furthermore, several of the different protein variants have been associated with milk production and with fat and protein yield and percent-

ages (Ng-Kwai-Hang et al., 1984, 1986; Aleandri et al., 1990; Bovenhuis et al., 1992; Tsiaras et al., 2005). However, many contradictions in their effects exist in the literature, and it is not clear whether the protein genes or linked genes produce the effect (Bovenhuis et al., 1992).

The shape of the lactation curve became a trait of interest for selection once again because of issues of cow health from the stress of high peaks in production and for use in an index to improve total yield. Aspects of the lactation curve considered by Shanks et al. (1981) included the lactation curve, persistency, week of peak yield, and peak yield. Generally low heritabilities were found, except for peak yield, which had heritabilities ranging from 0.16 to 0.23. Ferris et al. (1985) reported low heritabilities with large standard errors for lactation shape measures, and indices formulated to flatten the lactation curve did so at the expense of milk yield. Jamrozik et al. (1997) applied random regression models to test-day yields to generate EBV for partial-lactation yields and persistency for animals with even single test-day records. Genetic evaluations are now performed in several countries for lactation persistency.

Much success has been achieved in the improvement of production traits as a result of genetic selection. The dominant role production traits held in selection programs for many decades has been diminishing as selection goals become broader. Selection for production traits needs to be examined in tandem with relevant nonyield traits.

CONFORMATION

Conformation, or type, of an animal has been of interest to dairy producers since the beginning of the selection process. The archetypes for conformation and beauty in dairy cattle have been passed down through time and conveyed from past breeders (Copeland, 1941). Producers strongly considered conformation traits for breed standards of perfection for registration and in the show ring as well as to garner top prices in public sales. The aesthetic aspect of the animal was the main reason for selection, but conformation traits were increasingly used to select dairy cows for other characteristics, such as higher production and longevity.

Several breed associations started classification programs to appraise conformation of all animals in the registry based on a scorecard or scale of points. In 1929, Holstein cattle in the United States were classified for 4 major categories: general appearance, dairy character, body capacity, and mammary system. Soon after, in 1932, the American Jersey Cattle Club established a similar classification program. The data collected through the classification programs confirmed an exist-ing relationship between conformation and producing ability, highlighting the fact that both conformation and production should be considered in selection programs (Copeland, 1938).

The stability of conformation classification and the repeatability of the measurement were questioned in early studies (Johnson and Lush, 1942; Hyatt and Tyler, 1948). For example, Johnson and Lush (1942) reported high variation between evaluators and low repeatability for conformation traits ranging from 0.34 to 0.55. The heritability estimates reported for conformation traits were moderate to low. Tyler and Hyatt (1948) reported a heritability estimate for conformation of approximately 0.30. O'Bleness et al. (1960) reported heritability estimates for 27 different conformation traits ranging from 0.00 to 0.33.

In an effort to establish a more objective way to measure conformation traits, studies were conducted using data recorded from a conformation appraisal program initiated in 1953 in New York. The studies showed effects of appraiser (Van Vleck and Albrectsen, 1965), age, and lactation stage (Norman and Van Vleck, 1972) on conformation trait measures. Using data from the same appraisal program, Van Vleck (1964b) estimated heritabilities for conformation traits higher than those estimated previously and much closer to those reported in more recent studies (e.g., Rupp and Boichard, 1999).

In 1967, the Holstein-Friesian Association of America introduced a descriptive classification program that included an assigned code value for 12 conformation traits in addition to the 4 scorecard traits already recorded since 1929. These measures were also recorded on unregistered cows. The implementation of this system provided a large amount of data, allowing a more precise evaluation of conformation traits. Because of their negative correlation with milk production, conformation traits should be included in selection objectives to maintain cow appearance (Grantham et al., 1974).

Due to increased attention on linear conformation appraisal in the 1980s, a substantial change occurred in the methods used for estimating genetic values for conformation traits. The aim was to score conformation traits using a wider range of numerical scores (i.e., a 50-point basis). This measurement method presented several advantages, the major one being that it allowed analyses on a continuous scale and with mixed-model evaluation, as described by Thompson et al. (1983).

The predictive ability of conformation traits for additional traits of interest, other than production or longevity, was considered in several studies. Udder conformation traits showed varying but usually positive correlations with milking ability (Blake and McDaniel, 1979) and favorable correlations with udder health (Monardes et al., 1990; Rogers et al., 1991). As well,

mostly favorable correlations have been found between conformation and fertility (Dadati et al., 1985, 1986). The relationship between conformation and calving ease was negative when considering the conformation of the calf and positive when considering the conformation of the dam (Cue et al., 1990).

LONGEVITY

Longevity in dairy cattle has many different definitions and encompasses traits referring to the length of time a cow remains in the productive herd or its ability to remain in the herd. Measures of longevity have included age at disposal or last calving, number of lactations, and survival to a fixed age or lactation number. Cow longevity is a fundamental component of profitability in dairy production and, apart from production traits, has the greatest economic value (Allaire and Gibson, 1992). Longevity reduces the costs of replacements and maximizes the profitable period following the recovery of initial breeding and rearing costs. In addition, improving longevity could aid in breed development and genetic improvement because it would allow for more voluntary culling and greater selection intensity if fewer replacements were required.

The main goal in selecting for longevity is to decrease the premature disposal of cows or involuntary culling. By reducing the involuntary culling rate, dairy producers can consequently increase the voluntary culling rate and keep only the most productive animals. Reasons and strategies for culling are vast, may differ between years, and vary greatly between producers because they depend on the situation of the herd and involve a great degree of subjectivity and personal preference. Cows may be removed for voluntary reasons such as herd reductions, old age, level of production, body or conformation, management or workability, and sale for beef. Involuntary culling may occur for various reasons including reproductive performance, general health or illness, injuries, and accidents. Therefore, selection for longevity incorporates the improvement of many different components.

Automatic selection for increased longevity is presumed because cows remaining in the herd longer would produce more progeny and thereby contribute more to the succeeding generations (Parker et al., 1960). Because of the aforementioned importance of the trait to producers, further deliberate and direct selection for longevity was attractive and warranted. Measures of longevity were more easily recorded and accessible than records for fitness traits. Asdell (1951) examined DHIA herd culling records and stated that work needed to be done to develop longer living cows and reduce the loss of aging cows to sterility and udder troubles,

which were on the rise. When studying the occurrence of cystic ovaries in a herd, Casida and Chapman (1951) found that there was a significant daughter–dam correlation for time spent in the herd. Wilcox et al. (1957) estimated in a single herd a heritability of 0.37 for longevity measured as number of parturitions. In a herd that had experienced no deliberate selection for conformation or production, Parker et al. (1960) found a near-zero heritability for longevity in terms of age at last calving. In general, the heritability of longevity in dairy cows is low (White and Nichols, 1965; Miller et al., 1967; Hargrove et al., 1969; Schaeffer and Burnside, 1975; Ducrocq et al., 1988; VanRaden and Klaaskate, 1993). Variation in reported heritabilities could be attributable to single or small numbers of herds used in early studies and differences in culling reasons between the populations.

To qualify a direct record for longevity, the cow or daughters of a sire must have reached the end of their productive life, which means the cow is no longer available and the generation interval is increased in evaluated sires. To overcome this and the low heritability, early measures for indirect selection for longevity were investigated. Parker et al. (1960) found a significant correlation between first-lactation fat production and longevity recorded as age at last calving. Gaalaas and Plowman (1963) found a tendency for better producing young cows to stay in the herd longer using an intrasire regression of age at last calving on production. The propensity for high first-lactation producers to complete more lactations was substantiated by Van Vleck (1964a), White and Nichols (1965), and Hargrove et al. (1969), indicating that selecting young sires on daughter first-lactation production records would indirectly improve longevity. This conclusion was in contrast to the belief of many producers, who thought that many young high-producing cows leave the herd early and do not live up to this high production later in life (Van Vleck, 1964a).

The physical characteristics of a dairy cow were assumed to be related to its longevity. Conformation traits were widely available for classified cattle, known early in life (usually first lactation), and heritable, making them attractive indicators of longevity. Specht et al. (1967) reported a correlation of 0.20 between overall first classification score and longevity of Holstein-Friesian cows. They found similar correlations between individual conformation traits and longevity. Using the daughters of AI sire Holsteins, Van Vleck et al. (1969) examined the relationship between 66 type categories measured in first lactation and longevity, determined as number of recorded lactations. The type traits with the strongest correlations with longevity were plumb rear teat position (0.38), sharp dairy character (0.35),

intermediate thurls (0.26), and typical head (0.25). Schaeffer and Burnside (1975) looked at sire proofs for the survival rates of 2-yr-old daughters making a record at 3 and 4 yr of age and resolved that improvement in longevity could best be achieved using type and milk proofs opposed to longevity directly. With the arrival of linear type traits, more research into their correlation with longevity was completed. Several studies highlighted the relevance of many udder characteristics, feet and legs, and dairy character in improving selection for longevity (Rogers et al., 1988; Foster et al., 1989; Short and Lawlor, 1992).

An improvement of the longevity definition was suggested to better direct selection toward increasing the ability of cows to survive irrespective of production (Van Arendonk, 1986). Miller et al. (1967) examined longevity by dividing cows into opportunity groups to enable comparisons before all cows had died and further adjusted longevity for milk production. They found that heritabilities decreased when the effect of first-lactation milk was removed. Later, Ducrocq et al. (1988) suggested 2 measures of longevity: (1) true longevity not adjusted for yield, describing the ability of the cow to remain in the herd, and (2) functional longevity, linearly adjusted for the cow's milk yield relative to the herd, representing the ability to delay involuntary culling. The correction of longevity for milk production should expose differences between animals culled for nonproduction reasons. Given culling levels for production, adjustment of longevity for production was recommended to eliminate bias from culling for production (Dekkers, 1993).

Research over the past decades has shown that longevity is heritable and that selection is possible. Thus, many major countries in dairy breeding have included longevity in routine genetic evaluations (Miglior et al., 2005). Multiple-trait evaluations combining indirect measures of longevity with direct measures are helpful to improve the accuracy of longevity evaluations. There is currently no consensus in the trait definition and methodology for evaluation across countries. The United States considers productive life, which combines direct longevity defined as total months in milk through 84 mo of age, along with SCS, udder, body size, feet and leg composites, and milk, fat, and protein yields (Cruickshank et al., 2002). In Canada, genetic evaluations for direct longevity are from a 5-trait animal model including cow survival from first calving to 120 DIM, from 120 to 240 DIM, from 240 DIM to second calving, survival to third calving, and survival to fourth calving to account for differences in the genetic background of survival at different time points (Sewalem et al., 2007). Complementary indirect longevity evaluations in Canada are based on dairy strength, feet and legs, overall mammary, rump angle, SCS, milking speed, nonreturn rate in cows, and interval from calving to first service (Sewalem et al., 2007). In the future, the incorporation of additional traits relating to longevity, which includes many health traits, may benefit evaluation and selection for longevity.

FERTILITY

Because of the economic importance of reproductive efficiency, much attention has been given to fertility traits and to their relationship with production over the years. Moreover, genetic correlation with productive life indicates that fertility plays a major role in longevity of the cow (VanRaden et al., 2004). The advent of AI activities actualized the problem of fertility, and the possibilities of breeding for reproduction had to be investigated in a completely new light. Principally, the attention and research on fertility has been directed toward female fertility. The consequences and variation in sire fertility are seldom regarded in the genetic improvement of fertility. This is despite the fact that different fertility measures in dairy breeding can be affected by only the cow or bull or a combination of both male and female fertility, such as conception rate. Early measures of female fertility were the number of services required for conception, nonreturns to first service, the interval from calving to first insemination, and calving interval. The disadvantages of interval from calving to first insemination were that it might be influenced by farmer decisions or by seasonal calving. A late insemination could also be the result of estrus detection failure, so that the cow was cycling successfully but did not have the opportunity to conceive. On the other hand, success traits such as nonreturn rate may be affected by culling decisions made after first insemination, lack of recording of natural services, and inseminations made some days after first insemination. One of the earlier studies to address the genetic aspect of the problem of infertility was that of Spielman and Jones (1939), in which a correlation of 0.55 was reported between the reproductive efficiency of the cow and its female descendants. This suggested that the reproductive efficiency of the cow is an important factor in determining the mean reproductive efficiency of its offspring. The possibility of selecting for reproduction efficiency, however, was later questioned by several studies due to the very low heritability estimates reported for most of the considered fertility traits. Trimberger and Davis (1945) stated that even if a certain variation was found between both families and bulls, the number of services required for previous conceptions of the dam could not be used for predicting the breeding efficiency of the daughters. Dunbar and Henderson (1953) reported a

heritability of 0.004 for nonreturn rate at 180 d to first service. In the same study, the heritability estimate for calving interval was zero. Selection for fertility measured by nonreturn to first service, services required per conception, or calving interval was not very effective. Despite a low heritability for these traits, most measures of genetic variation, expressed in this relative way, were substantial and were often almost as large as those for milk yield (Philipsson, 1981). Similarly, the additive genetic variation for reproductive traits is greatly masked by a huge phenotypic variance, and it appeared unwise to ignore reproductive performance in selection programs for dairy cattle (Hermas et al., 1987). Furthermore, Raheja et al. (1989) estimated a heritability of 0.12 for age at first insemination, indicating that selection for this trait would result in a genetic response. Generally, the large residual variation observed for fertility traits is possibly attributable not only to the large effect of the environment and management on these traits but also to the low quality of the data, which represents an issue in the analyses of reproduction data.

The relationship between heifer fertility and cow fertility has been questioned for a long time. Philipsson (1981) reported that the fertility of a virgin heifer, a first-lactation cow, and an older cow might be different traits. Repeatabilities shown by Hansen et al. (1983) for virgin heifers and first-parity fertility suggested that heifer and cow fertility might not be highly related. More recent studies considered the genetic correlations between traits observed in both heifers and older cows and concluded that heifer and cow fertility traits were not genetically the same (Jamrozik et al., 2005).

The correlation between reproduction traits and milk production has been extensively studied. An antagonistic correlation between female fertility and milk production has been reported in several studies over the years (Everett et al., 1966; Miller et al., 1967; Berger et al., 1981; Oltenacu et al., 1991; Dematawewa and Berger, 1998; VanRaden et al., 2004). However, the effect of selection for milk on reproduction was controversial in the beginning because some studies reported little or no relationship between yield and reproduction (Weller, 1989). Even if an antagonistic relationship between female fertility and milk yield existed, the correlated response on fertility due to selection on lactation production would not be significant (Everett et al., 1966; Miller et al., 1967; Shanks et al., 1978). However, because milk yield was the predominant goal in dairy cattle selection, the long-term selection for yield may have caused deterioration of reproductive performance (Nebel and McGilliard, 1993). Later, it became accepted that due to unfavorable genetic correlations, selection for higher yields in dairy cattle has possibly led to a decline in fertility (Pryce et al., 2004) as the reproduction physiology of dairy cattle changed in response to genetic selection for milk production (Lucy, 2001). The inclusion of reproductive measures in the general indices was adopted relatively late, mostly due to data availability. Genetic evaluation for reproduction was first adopted in the Nordic countries, which started to include reproduction traits in national indices in the late 1970s. Female fertility has been included in the total merit index for Norwegian dairy cattle since 1972 by considering the 56-d nonreturn rate in virgin heifers; since 2002, the 56-d nonreturn rates in first-lactation cows have also been considered (Andersen-Ranberg et al., 2005). Nordic countries remained the only ones to consider these traits for many years. According to a survey published in 1994, they were still the only countries to consider fertility, calving performance or stillbirth, and health traits in their total merit index (Philipsson et al., 1994). In a more recent survey referring to data from 2003, Miglior et al. (2005) reported that more countries included fertility in their national selection indices, including several European countries, Australia, New Zealand, and the United States, showing a shift of selection emphasis in the last decade from mainly production to functional traits associated with health and fertility.

Because of the low heritability of fertility traits and the difficulties related to their measurement, indicator traits could be very useful for increasing accuracy of EBV for fertility. Novel phenotypes, such as BCS, have been proposed as indicator traits for fertility. A strong relationship was found between BCS and reproductive measures (Pryce et al., 2001; Veerkamp et al., 2001; Berry et al., 2003; Bastin et al., 2010). Also, some recent studies have explored the possibility of taking advantage of more recently available data, such as the mid-infrared (**MIR**) predicted fatty acid profile in milk. Bastin et al. (2012) observed moderate correlations between C18:1 *cis*-9 fatty acid (an indicator of body fat mobilization) and days open at 5 and 200 DIM (0.39 and −0.38, respectively).

CALVING

Under normal circumstances parturition in cattle should terminate without human interference, leaving a healthy cow and a viable calf. A significant proportion of calvings, however, are assisted to a major degree and could yield a stillborn calf (Meijering, 1984). Stillbirth commonly includes calf mortality shortly before, during, or within 24 to 48 h after parturition (Philipsson, 1976). The selection focus for early-maturing cows over the past years could accentuate calving problems, especially as young animals calve for the first time well

before they reach their mature size. Calving difficulty and calf mortality represent major problems affecting profitability of dairy farming, and the economic loss is associated with various factors. Dystocia was reported to have a negative effect on 305-d milk, fat, and protein yields, days open, number of services, and cow losses (Dematawewa and Berger, 1998). The eventual death of the calf is also costly, especially if the dead calf is female. Several countries reported increasing stillbirth rates for Holsteins between 1985 and the late 1990s (Meyer et al., 2001; Steinbock et al., 2003; Hansen et al., 2004).

Calving ease is a combination of 2 different traits: direct calving ease, which is related to the calf, and maternal calving ease, which expresses how easily the cow gives birth. Pollak and Freeman (1976) reported a heritability of 0.08 for dystocia, defined as prolonged or difficult parturition. A decline in heritability estimates with increasing parity was also observed (0.18, 0.08, and 0.05 for first-calf, second-calf, and older cow records, respectively). Calf size had a heritability of 0.15 and showed a strong genetic correlation with dystocia (0.97). Berger and Freeman (1978) reported that including relationships due to sire and maternal grandsire of bulls with progeny data and accounting for the unequal variance associated with parity of dams increased the precision of individual sire estimates and resulted in a higher heritability for calving difficulty, which was estimated at 0.12. The relationship between dystocia for primiparous and multiparous cows has been controversial. Early studies (Thompson et al., 1981; Boldman and Famula, 1985) reported very strong correlations between dystocia in primiparous and multiparous cows (0.84 and 0.99, respectively). However, Weller et al. (1988) reported that the correlation between first-parity and later-parity sire evaluations was lower than 0.50. Steinbock et al. (2003) estimated heritabilities for stillbirth of 0.04 and 0.03 for the direct and maternal effect, respectively. Heritabilities for calving difficulty were 0.06 for direct effect and 0.05 for maternal effect. At second calving, the corresponding heritabilities for the 2 traits were considerably lower (<0.01). Despite low heritabilities, a substantial genetic variation in both traits, expressed by differences between EBV of bulls, was observed for first calvers. Heringstad et al. (2007) reported strong genetic correlations between direct stillbirth and direct calving difficulty (0.79) and between maternal stillbirth and maternal calving difficulty (0.62). All genetic correlations between direct and maternal effects within or between traits were close to zero, suggesting that bulls should be evaluated both as sire of the calf (direct) and sire of the cow (maternal). Thompson et al. (1981) suggested that selecting for reduced dystocia, considering only the direct effects,

would reduce genetic progress for this trait. These conclusions were based on negative correlations found between direct and maternal effects (−0.38 and −0.25 for heifers and cows, respectively). Similar results were also reported by Boldman and Famula (1985), who estimated genetic correlations between direct and maternal effects of −0.40 and 0.07 in heifers and adult cows, respectively. Dekkers (1994) concluded that the optimal breeding strategy for calving ease would be to select sires based on an index that includes EBV for both direct and maternal calving ease along with other traits of economic importance.

Nordic countries were the first to consider calving performance and stillbirth in their national indices (Philipsson et al., 1994). Evaluations for calving ease traits, however, were also available early in other countries. For example, the evaluation of service sire calving ease has been published in the United States since 1978, whereas daughter calving ease was not implemented until 2002 (Shook, 2006). The first sire evaluations for calving ease for bulls used in Ontario, Canada, were published in 1981 (Cady and Burnside, 1982).

HEALTH

Diseases in dairy cattle are a major source of economic loss for dairy producers. Loss is a result of reduced production, death, premature culling of animals, veterinary treatments, lost milk due to antibiotic use, added labor, delayed conception, reduced genetic gains, low milk quality, and increased susceptibility to other diseases. More recently, heightened concerns over antibiotic use and ethical and animal welfare matters have added further demand for health traits to be included in breeding programs. Although there is a large effect of environment and management on disease occurrence, variation between cows can be observed.

Mastitis, the most prominent and economically significant disease affecting the dairy industry, received early attention from animal breeders because reducing its occurrence using all possible approaches was warranted. Unfortunately, mastitis can be caused by different species of bacteria and can occur in one or more quarters of the udder. Management conditions at the herd level can also have a large effect on the presence of mastitis. Lush (1950) first studied the possible inheritance of mastitis resistance by examining cows that developed mastitis at any age and those that had not developed mastitis by the age of 8 yr. Susceptibility to mastitis was found to have a strong genetic background, and Lush concluded that the incidence of mastitis could be reduced by selecting against severely affected cows or those with severely affected sisters or daughters. Legates and Grinnells (1952) also found

mastitis resistance to be heritable based on rating cows as infected or not through the study period.

Casida and Chapman (1951) investigated the incidence of cystic ovaries in a US Holstein herd and estimated a heritability for the occurrence of cystic ovaries some time in a cow's life as 0.43. An inherited component of ketosis, which also caused high economic loss, was also implicated, but Shaw (1956) stated that this component was not of primary importance in most herds and that more reports and evidence were required. These early appraisals of the role of genetics in mastitis and other disease susceptibility were hampered by limited data and highlighted the need for improved phenotypes and methods for earlier evaluation.

Young et al. (1960) studied the genetic relationship between clinical mastitis and the additional phenotypes of bacterial infection, leucocyte count, and udder and hock height alongside clinical diagnoses of mastitis. A significant negative genetic correlation was reported between clinical mastitis and udder height. Most significantly, their results using daughter–dam data indicated that including leucocyte score in an index would increase the efficiency 140% over using clinical mastitis alone. Somatic cell counts were introduced into many milk recording programs in North America and Europe in the late 1970s, raising renewed interest and serious discussion on selection for mastitis resistance. Ali and Shook (1980) demonstrated that a log-transformation of SCC to produce a score (SCS) resulted in a near-normal distribution of SCC and greater heritability. Kennedy et al. (1982) estimated an average heritability of 0.08 for SCS and small, undesirable positive genetic correlations between SCS and yield traits. Heritabilities for SCS reported by Coffey et al. (1985) ranged from 0.09 to 0.29 depending on parity. Additional work by Coffey et al. (1986) approximated genetic correlations between SCS and measures of infection to be between 0.36 and 0.67, providing further evidence that genetic evaluation and selection for decreased SCC may aid in reducing mastitis incidence. Originally purposed as a management tool and milk quality criterion, SCC found its place in genetic selection because of ease of measurement, a moderate heritability, and an association with both clinical and subclinical forms of mastitis. However, Coffey et al. (1986) expressed concern at the time that the consequences on selecting for decreased SCC were not understood and could, in the long term, lead to a reduction in the response to udder infection if SCC were too low. Another apprehension in the implementation of selection for mastitis resistance was the well-known antagonistic genetic relationship between mastitis traits and yield traits (Kennedy et al., 1982; Coffey et al., 1986; Emanuelson et al., 1988). Shook (1989) discussed that the decreasing genetic

trend in cow health due to selection for yield was a major concern, especially when considering long-term projections, and this should be a convincing reason to consider mastitis resistance in breeding programs.

In Nordic countries, where only veterinarians are allowed to treat animals, nationwide systems for health data recording were established in the 1970s. These databases contain reliable records for disease treatments on a national scale, and many traits were subsequently added into routine genetic evaluations (Heringstad et al., 2000; Philipsson and Lindhé, 2003). In health data recording programs, a large number of disease traits are recorded, the most prevalent being mastitis and ketosis. Heritabilities of various health traits have been generally low but sufficient to allow for selection for reduced health problems (Emanuelson et al., 1988; Lyons et al., 1991; Simianer et al., 1991; Uribe et al., 1995; Pryce et al., 1997).

In countries with no regulated systems in place for dairy cattle health recording, obtaining sufficient records of health events for genetic evaluation recounts the issues of too few data experienced by early researchers. Zwald et al. (2004) began to look at health data recorded by American dairy producers in on-farm management software programs for mastitis, lameness, cystic ovaries, and metritis. Low heritabilities were found, but these data provide useful information for selection purposes, especially for incidence of any disease in the first 50 d postpartum. In Canada, a national dairy cattle health and disease data management system was started in 2007 for voluntary producer recording of 8 diseases: mastitis, displaced abomasum, ketosis, milk fever, retained placenta, metritis, cystic ovaries, and lameness (Koeck et al., 2012). Producer-recorded health data can be used in genetic evaluations, but sufficient participation and accurate and complete health records are necessary.

Health records could provide important information for genetic selection programs, but low heritabilities, nonnormal distributions, and subjectivity in diagnosis made potential indicator traits appealing. Emanuelson et al. (1988) examined Swedish mastitis treatment records and found enough genetic variation to attain significant genetic improvement if records on enough progeny of a sire were available. They also resolved that SCS should be used in selection. Somatic cell score became the trait contributing to udder health selection indices, with some countries also including evaluations for udder conformation traits, milking speed, clinical mastitis, and dairy form (Miglior et al., 2005). Indicators for selection and the genetic evaluation of metabolic diseases, including ketosis and displaced abomasum, have been discussed by Pryce et al. (2016). For ketosis, acetone was considered to be an indicator for disease,

but low heritabilities estimated for its content in milk suggested little genetic control (Emanuelson and Andersson, 1986; Wood et al., 2004; van der Drift et al., 2012). Another indicator of subclinical ketosis, milk BHB, can be predicted using MIR spectroscopy during milk recording, although with limited accuracy. Heritabilities for milk BHB have ranged from about 0.07 to 0.16 (van der Drift et al., 2012; Koeck et al., 2014; Jamrozik et al., 2016). Milk BHB and other heritable indicators (fat-to-protein ratio and BCS) are genetically correlated with clinical ketosis and displaced abomasum and are used in multitrait genetic evaluations for metabolic diseases (Koeck et al., 2014; Jamrozik et al., 2016). Predictor traits have been an integral component in multiple-trait evaluation of health traits in breeding programs to generate higher EBV reliabilities.

The concern over the genetic decline in dairy cattle health has brought attention to genetic selection for improved health, and research continues on the identification of new traits to aid in this selection goal. Mainly, only individual diseases with high incidence have been included in selection programs thus far, and many health traits would benefit from more records or multitrait evaluation with indicator traits to improve the accuracy of genetic evaluations. Potential future predictor traits for health traits could include on-farm or laboratory measures. Energy balance is associated with many metabolic diseases as well as fat-to-protein ratio (Jamrozik et al., 2016), and it has been examined in regards to change in BCS (Roche et al., 2009). Energy balance can be predicted directly using MIR spectroscopy (McParland et al., 2014) or indirectly from milk fatty acid content (Berry et al., 2013). Other potential areas for exploration could involve information from various on-farm sensor systems, including cow activity and milk traits (Rutten et al., 2013), milk component analysis (Hamann, and Krömker, 1997), and genomic markers, among many others.

WORKABILITY

Traits that facilitate working with cows on the farm are categorized as workability traits; the most important ones are temperament (or, more generally, behavior) and milking speed because they have economic effects on the production system (Schutz and Pajor, 2001). As discussed by Schutz and Pajor (2001), various researchers have contributed to the estimation of genetic parameters for dairy cattle behavior and other workability traits, indicating the potential for genetic selection. Heritability estimates presented for temperament ranged from 0.08 to 0.25. Various decades ago, O'Bleness et al. (1960), Markos and Touchberry (1970), and Touchberry and Markos (1970) indicated a poten-

tial to genetically select for the improvement of milking speed scores, milk flow, and time required to milk cows. In addition, differences among breeds were noted. For instance, Burnside et al. (1971) reported genetic variation among breeds for the percentage of cows culled for bad temperament.

Tomaszewski et al. (1975) assessed several measures of milking rate to determine which variable would be most practical as a field measure. Milking rates were estimated by peak flow; average flow; percentage of milk produced in the first 2 min of machine milking; and the amount of milk produced in the first 1 min, first 1.5 min, and first 2 min of milking. They concluded that the percentage of the total milk produced at 2 min of milking was an adequate field measure of milking rate. After that, Miller et al. (1976) reported genetic parameters for various measures of milk flow rate and milking time. They estimated heritabilities for peak rate, average rate, total time, duration of peak rate, and yield during peak rate of 0.47, 0.37, 0.17, 0.10, and 0.07, respectively. Direct selection for peak rate would provide an opportunity to reduce total milking time.

Agyemang et al. (1982) estimated variance components for various workability traits. They also defined some novel workability traits such as overall satisfaction, which was based on the opinion of producers on whether they would like another cow like the one in question. Erf et al. (1992) also defined additional workability traits, including trouble-free workability and overall satisfaction, which had heritabilities of 0.11 and 0.08, respectively. The majority of early studies investigating workability were based on subjective scores. To limit the subjectivity of workability evaluations, Moore et al. (1983) proposed the use of additional objective measures to increase the accuracy of genetic evaluation for milking speed. These were based on the trait "2-min milk" as well as the total milk duration for each animal. Williams et al. (1984) also presented genetic parameters for these traits (e.g., h^2 for 2-min milk = 0.25) in a different population. Meyer and Burnside (1987) suggested the measurement of repeated records for milking speed because genetic and environmental factors that affect milking speed of individual cows may vary during lactations or between subsequent lactations.

Visscher and Goddard (1995) reported heritability estimates for milking speed, temperament, and likeability to be between 0.18 and 0.29. Rupp and Boichard (1999) reported moderate heritabilities for milking ease recorded by producers. Wiggans et al. (2007) and Sewalem et al. (2011) also reported heritabilities for milking temperament and milking speed ranging from 0.13 to 0.22. Analysis of bull proof correlations of temperament and milking speed with other traits gave low correlations with traits such as production,

reproduction, conformation, and auxiliary traits. Various countries have already included milking speed and temperament in their breeding objectives for more than 20 yr (Miglior et al., 2005).

Lin et al. (2013) investigated various indicator traits for feed behavior and its relationship with feed efficiency. The traits studied were number of meals, feeding duration, DMI, eating rate, and average meal size. Kramer et al. (2013) reported updated genetic parameters for general temperament, milking temperament, aggressiveness, rank order in herd, and milking speed, which were low to moderate, indicating the possibility for selection.

Workability traits are becoming more relevant due to robotic milking systems, which are becoming more common in the dairy industry (Chesnais et al., 2016). Traits aimed toward a cow's suitability to automatic milking systems are now under consideration for selection, including milk yield per minute of box time, milking interval (the time between 2 consecutive successful milkings), and habituation of heifers (the time for a primiparous cow to get familiar with automated milking systems; Vosman et al., 2014). Despite the progress made, a better understanding is needed of the genetic mechanisms of various behavior traits that allow dairy cattle to be more adapted to modern production systems.

NOVEL TRAITS

For a long time, selection in dairy cattle focused on the improvement of highly heritable production and conformation traits. As shown in Figure 1, heritabilities for both production and conformation traits are markedly higher than those for traits included later on. Figure 2A presents a schematic representation of how an average selection index has evolved over time in terms of relative emphasis for traits under selection. Selection goals have since broadened to include economically important traits with low heritability, partly due to the realization that such traits can indeed be genetically improved and partly due to the fact that modern and automated technologies provide more data. Selection for production, and partly for conformation, has resulted in indirect negative response in health and fertility, as shown in Figure 2B. To counteract those negative trends, health and fertility were included in selection indices, and their relative emphases have gradually increased at the expense of production and conformation. Since the inclusion of functional traits in selection indices, the detrimental effects of narrow selection goals have been counteracted, and we are currently making genetic progress in all traits of economic interest.

The power of genetic improvement is noticeable, as a desirable genetic progress has been increasingly observed since the inclusion of those traits in selection indices worldwide, especially with the introduction of genomic selection. To ensure continued progress and to develop breeding goals more in line with producer and consumer expectations, the inclusion of novel traits can be considered. Rapid advancements in technology and methodology related to the dairy industry have fueled new opportunities to include new traits in the breeding goal. In particular, the implementation of genomic selection accelerated progress in novel trait selection. In addition, the use of MIR spectroscopy in routine milk testing has expanded in many countries to predict new traits and generate large numbers of phenotypes in an inexpensive manner. The traits considered for selection continue to evolve as the industry changes; many novel traits are currently being considered around the world and are at various stages of development.

Feed Efficiency

Feed represents a large proportion of dairy cattle production expenses. Generally, feed efficiency describes units of product output per unit of feed input, with the units generally being mass, energy, protein, or economic value (VandeHaar et al., 2016). Koch et al. (1963) described a measure of feed efficiency, residual feed intake (**RFI**), that is independent of an animal's body size and production level and is considered to represent the inherent variation in basic metabolic processes that determine efficiency. As reviewed by Connor (2015), heritability estimates for RFI in lactating cows range from 0.01 to 0.40. For some time, feed intake was estimated based on BW and production. However, Gibson (1986) presented a correlation between true feed efficiency and predicted feed efficiency (derived from BW and production) of 0.84, indicating that there could be value to actually measuring feed intake. In the 1990s, there was great interest from the industry in including feed efficiency in dairy breeding objectives, which motivated various organizations to collect individual feed intake records for research and genetic evaluations, as described in various studies (Van Arendonk et al., 1991; Veerkamp, 1998).

Williams et al. (2011) reported that significant variation in RFI exists in growing heifers and that this could be an alternative to indirectly select dairy cows for improved feed efficiency because it is easier to record feed intake in growing heifers. Spurlock et al. (2012) estimated genetic parameters of various traits associated with energy balance and related traits, including DMI, BW, BCS, ECM production, and gross feed efficiency,
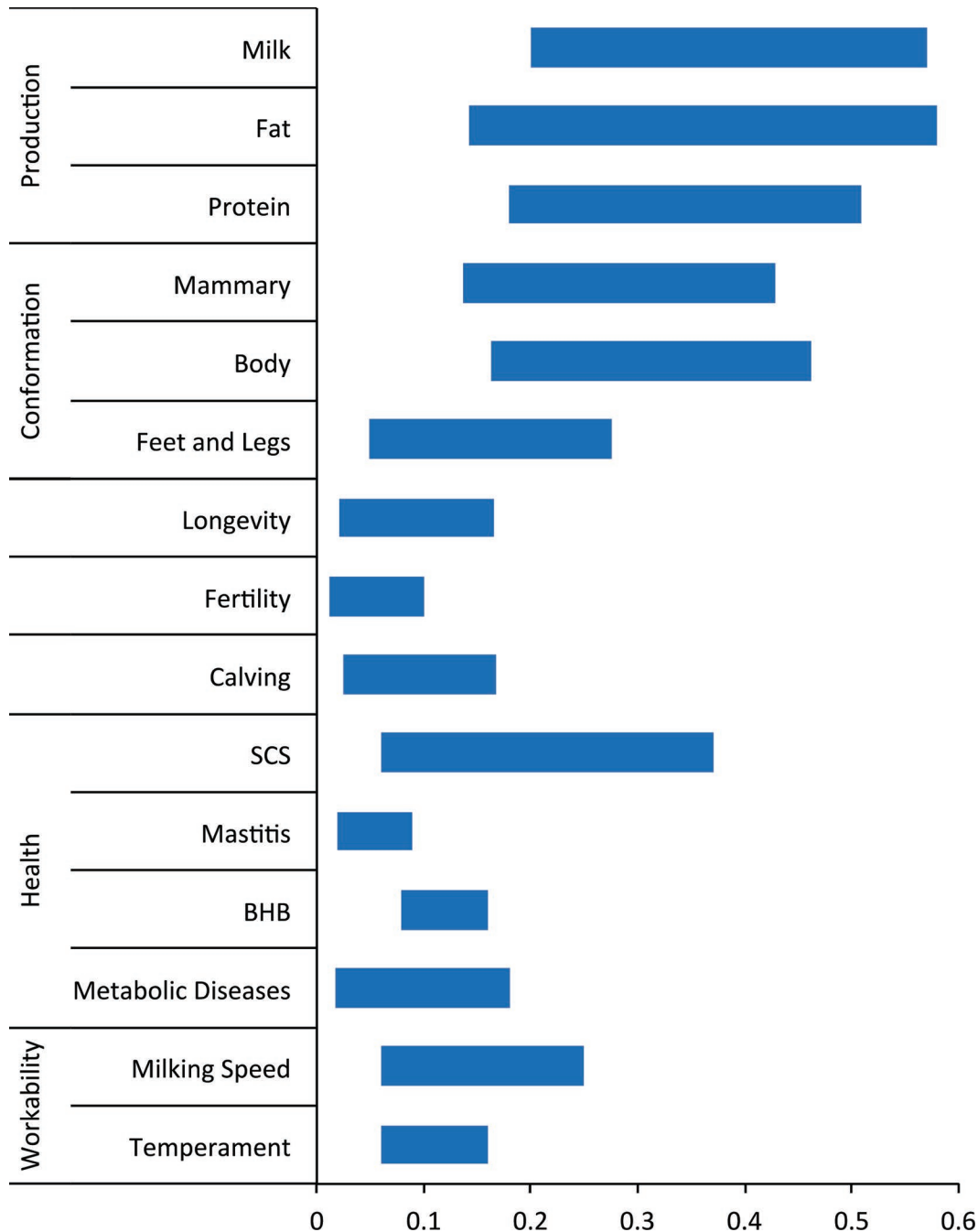
Figure 1. Ranges in heritabilities for various traits used in current Interbull evaluations (April 2017 run, Interbull, Uppsala, Sweden). Heritabilities for metabolic disease are for Nordic countries, the United States, and Canada only; heritabilities for BHB are for Canada and the Netherlands. Color version available online.

and suggested that these traits will likely respond to genetic selection in Holstein cows. A negative genetic correlation was found between gross feed efficiency and energy balance (from −0.73 to −0.99), indicating that selection for more efficient cows would favor a lower energy status.

Genomic selection has been a very important tool in the selection for increased feed efficiency in dairy cows. For instance, Gonzalez-Recio et al. (2014) described the implementation of heifer feed efficiency in the Australian selection index using genomic selection and its effect in the industry. Pryce et al. (2015) described the

implementation of genetic evaluation for Feed Saved, which combines RFI in growing calves and lactating cows with feed required for maintenance predicted from BW as a new indicator of feed efficiency in dairy cows. Since April 2015, Feed Saved has been included as part of the Australian national selection index.
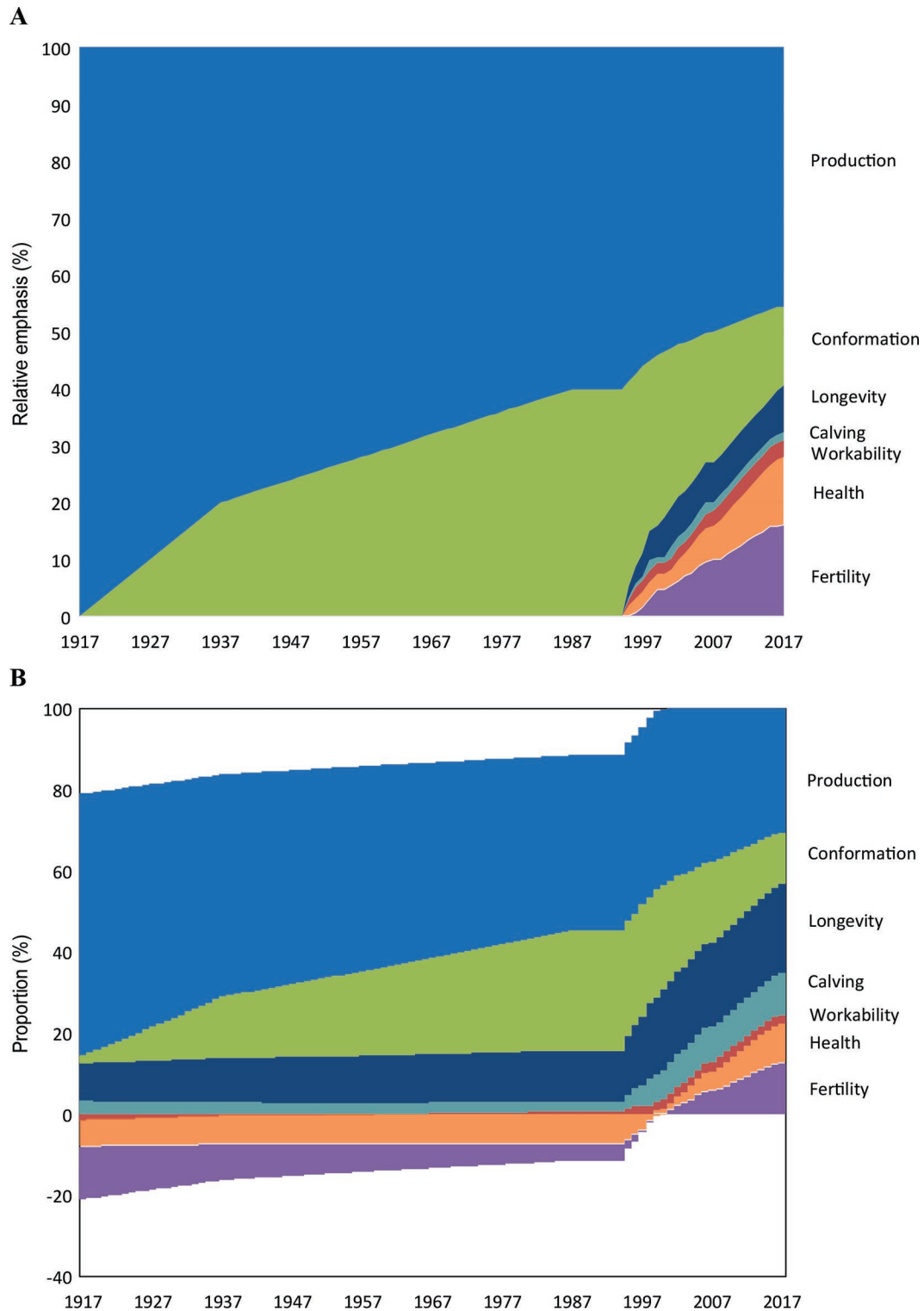

Figure 2. Schematic representation of (A) relative emphasis of traits included in an average selection index over time and (B) proportion of estimated selection response for various trait categories over time (summing to 100%). Color version available online.

Methane Emissions

Mitigation of enteric methane emissions in ruminants has become an important area of research because methane is strongly linked to global warming. Herd et al. (2002) reported variations in enteric methane emissions between animals and breeds and across time, indicating potential for improvement through genetic selection. In a study to predict methane production from dairy and beef cattle, Ellis et al. (2007) presented statistical models of methane production. Over time, various methodologies for measuring and estimating methane production in cattle were developed (Wall et al., 2010; Negussie et al., 2017). Several methane emission proxies and related variables include feed intake and feeding behavior, rumen function, metabolites and microbiome (rumen microbiota and host–microbiome interactions), milk production and composition, hindgut and feces, and measurements at the level of the whole animal, as reviewed by de Haas et al. (2017). de Haas et al. (2011) presented genetic parameters for predicted methane production and potential for reducing enteric emissions through genomic selection. Several studies have confirmed that methane emission is a moderately heritable trait ranging from 0.21 to 0.35 (de Haas et al., 2011; Lassen and Løvendahl, 2016).

Heat Stress

In a world with a changing environment, breeding robust dairy cows will likely become an important activity in the near future. Over time, studies have been performed to better understand dairy cattle adaptation to heat stress. Ravagnolo and Misztal (2000) reported that selection for heat stress is possible and could be particularly effective for environments with a high average temperature–humidity index. Ravagnolo et al. (2000) reported the usefulness of weather data in developing a heat-stress function suitable for studies on genetics of heat stress. More recently, Nguyen et al. (2016) demonstrated that heat tolerance in dairy cattle could be improved using genomic selection, and implementation of genetic selection for heat tolerance in the Australian breeding programs is under discussion. Tolerance to heat stress has been shown to be heritable, ranging from 0.17 to 0.33 (Nguyen et al., 2016).

Hoof Health

In the early 2000s, Warnick et al. (2001) and Booth et al. (2004), respectively, assessed the effect of lameness on milk production and dairy cow survival, indicating the importance of this trait for the dairy industry. Ge-
netic evaluations for feet and leg type traits have been available for several years in many countries. However, van der Waaij et al. (2005) and Chapinal et al. (2013) reported low genetic correlations between infectious claw lesions and feet and leg traits. These results partially explain why selection for improving hoof health by using conformation traits has not been effective so far and indicate the need to include direct indicators of hoof health in selection indices. Koenig et al. (2005) presented genetic parameters for different types of claw and foot disorders and the genetic relationship of disorders with milk yield and selected conformation traits. In the last 2 decades, other major contributions to the understanding of the genetic architecture of various indicators of hoof health and recommendations for genetic selection have been made, such as Boettcher et al. (1998), van der Waaij et al. (2005), Laursen et al. (2009), van der Linde et al. (2010), Oberbauer et al. (2013), and Malchiodi et al. (2017). Heritabilities of individual hoof lesions have ranged from 0.01 to 0.13 (Koenig et al., 2005; van der Spek et al., 2013; Malchiodi et al., 2017). A variety of approaches and phenotypes may be required for the improvement of hoof health. de Mol et al. (2013) investigated the feasibility of implementing a lameness detection model based on daily activity data and concluded that automated lameness detection based on day-to-day variation in behavior is a useful tool for dairy management.

Immune Response

The immune response or ability to resist infections and diseases is a complex trait of great economic importance for the dairy industry. Mallard et al. (1983) studied variation in serum immunoglobulins in Canadian Holsteins and concluded that selection to alter immunoglobulin content and reduce disease may be feasible and should be examined further. Mazengera et al. (1985) reported genetic parameters for bovine serum immunoglobulins, indicating that some variation in the parameters was under genetic control. Thompson-Crispi et al. (2012) estimated genetic parameters for cell-mediated and antibody-mediated immune response traits of Holstein cattle and explored the association of these traits with other economically important traits, including disease resistance. More recently, Denholm et al. (2017) presented genetic and phenotypic parameters for other indicators of immune response. Cellular immune-associated traits are heritable and repeatable. Genetic selection for cellular immune-associated traits could provide a useful tool for improving animal health, fitness, and fertility.

Milk Composition

The genetic variation in the composition of milk is of interest because of its effect on the nutritional value and technological properties of milk. Soyeurt et al. (2011) reported that the prediction of most major fatty acids has become feasible on a large scale via MIR spectroscopy, which can be used in routine genetic evaluation. The fatty acid profile of milk has been shown to be under genetic control. Heritability of milk fatty acid contents tends to decrease with an increase in carbon chain length (Bastin et al., 2011). In addition, SFA are more heritable than UFA (Soyeurt et al., 2008). Therefore, there is potential to alter the fatty acid profile of milk through selection. Some countries, such as Belgium, have started to consider these traits.

Minerals found in milk, such as Se, Ca, K, Zn, Mg, and P, contribute to several vital physiological processes. van Hulzen et al. (2009) observed differences between cows and herds in concentrations of minerals in milk and determined that concentrations of many minerals in milk could be changed by way of nutrition or through genetic selection.

Milk Coagulation Properties

Milk coagulation property traits have become of interest to the dairy industry because they influence the profitability of the cheese sector. Lindström et al. (1984) presented genetic parameters for milk coagulation properties. Subsequently, more than 20 studies have been published on variables influencing milk coagulation and how to genetically select for them, as presented in Bittante et al. (2012). The physical characteristics of milk that are important in cheese manufacturing, such as rennet coagulation time, curd firmness 30 min after rennet addition, and curd firming time, have been studied. A limiting factor in the implementation of routine genetic evaluation for these traits is the time and expense involved in collecting the phenotypes. However, Cecchinato et al. (2009) proposed the use of MIR spectroscopy predictions as indicator traits in breeding programs for enhanced coagulation properties of milk, which can be more affordably measured.

Reproductive Technology Traits

In the last decades, superovulation and embryo transfer have been widely used around the world to increase the genetic contribution of elite females. König et al. (2007) reported low to moderate maternal heritabilities for number of flushed ova, transferable embryos, degenerated embryos, unfertilized oocytes, and percentage of transferrable embryos. Recently, Jaton et al. (2016) investigated genetic parameters for the number of total and viable embryos produced per flush and concluded that there is genetic variability for these traits and potential for selection. Parker Gaddis et al. (2017) also investigated the genetic components of various traits related to reproductive technologies and found many regions of the genome associated with these traits, some of which correspond with those previously identified for fertility traits already evaluated in dairy cows.

NEXT DECADE

In the 1920s, the 305-d milk yield of an average North American Holstein cow was around 2,000 kg. One century later, the average Holstein cow produces more than 10,000 kg of milk, with fat and protein percentages similar to those of 100 yr ago. This 5-fold increase, attributable to enhanced management, feeding, and genetics, is one of the most successful stories of improvement in livestock production. The dramatic increase, however, has come at a cost in terms of fertility and health. To counteract this decline, selection goals are becoming more comprehensive as new phenotypes become available and cost effective to measure.

A pivotal development in regard to trait selection is the advent of genomics, which has revolutionized the dairy cattle industry and has provided a new opportunity to select for traits that were prohibitively expensive to measure in the past. Selected commercial herds may provide a new source of high-quality phenotypic information, which, in conjunction with genomics, can be used within a breeding program to genetically improve the national herd. The collection of detailed (possibly expensive) phenotypes for a sufficiently large reference population, paired with the corresponding genotypic information of those reference animals, allows accurate estimation of marker effects for a specific trait. Subsequent calculation of genomic breeding values in a group of selection candidates without phenotypes has thus become possible. The advantage is that those detailed phenotypes could have markedly higher heritability than previous related traits. Immune response is an example: estimates of heritability for producer-recorded clinical diseases are very low (mostly <0.05), whereas estimates of heritability for immune response traits are much higher (0.25–0.35). Measuring immune response and genotyping animals in a sufficiently large reference population allow estimation of marker effects, which can then be used to estimate direct genomic breeding values in a group of selection candidates. A further example could be the identification of new fertility phenotypes that are more tightly linked to the female reproduction cycle and embryo survival; the use of current fertility phenotypes (interval traits such as

days open, or conception rate estimates such as 56-d nonreturn rate) has failed to significantly enhance the fertility of our modern lactating cows. If we are able to improve overall cow health, however, fertility may consequently also improve—that is, the healthier the cow, the more fertile it is. Finally, the advent of genomics has also allowed the inclusion of feed efficiency in breeding goals. The ability to decrease feed waste and convert feed into milk more efficiently will have significant advantages for the whole dairy sector while decreasing the environmental impact of dairying.

One century of selection has mostly focused on increasing milk production of the dairy animal. With the exception of fat and protein percentages, milk properties and quality have not been considered in detail thus far. During the last decade, the use of milk MIR spectral data for prediction of fine milk components and milk coagulation properties has added a potential new selection opportunity to enhance the quality of milk for human consumption and cheese-making. This complex objective will have consequences for dairy processors farther down the milk value chain, who will need to communicate with dairy cattle breeders.

CONCLUSIONS

Over the past 100 yr, traits considered for genetic selection in dairy cattle populations have progressed to meet the demands of various stakeholders. At the turn of the 20th century, the focus was fixed on increasing milk production. By the end of the century, the emphasis had shifted toward a more balanced breeding goal and included longevity, fertility, calving, health, and workability traits. This shift represents an increased awareness and recognition of societal influence but also a better understanding of animal physiology. In the near future, fitness, animal health and welfare, milk quality, and environmental sustainability will be included in even more comprehensive breeding goals. In the longer term, on-farm sensors, data loggers, precision measurement techniques, and other technological aids will provide even more data for use in selection, and the difficulty will lie not in measuring phenotypes or gathering data but rather in selecting and weighting traits with producer-minded economic advantages.

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APPENDIX

Table A1. Major milestones in the study of genetic selection of dairy cattle

Date	Milestone	Reference
1920	Breeding decisions are mainly based on milk and fat yields from milk testing programs along with consideration of conformation.	Gowen, 1920; Meade, 1921; Burrington and White, 1925; Graves, 1925; Fohrman, 1926; Copeland, 1927
1930	Classification programs are instituted by breed associations.	Copeland, 1938
1943	Selection index approach is used for simultaneous selection of multiple traits.	Hazel, 1943
1950	Interest increases in the SNF portion of milk due to proposed changes to milk pricing strategies.	Richardson and Folger, 1950; Johnson, 1957
1970	Fertility and health traits are evaluated in Nordic countries.	Heringstad et al., 2000; Philipsson and Lindhé, 2003
1970	Calving traits are introduced.	Philipsson, 1976; Pollak and Freeman, 1976
1970	Milk protein contents measured in milk recording programs and genetic evaluations are available.	Biggs, 1967; Shook, 2006
1980	Somatic cell counts are used in selection for udder health indices.	Ali and Shook, 1980; Kennedy et al., 1982; Coffey et al., 1985, 1986
1980	Linear type appraisals for cattle are used.	Thompson et al., 1983
1990	Workability and longevity traits are added to national genetic evaluations.	Burnside et al., 1971; Tomaszewski et al., 1975; Moore et al., 1983; Meyer and Burnside, 1987
2000	Fertility traits are considered by many non-Nordic countries.	Miglior et al., 2005
2010s	Health trait evaluations using producer-recorded health data and their indicators are initiated in several non-Nordic countries.	Zwald et al., 2004; Koeck et al., 2012; van der Drift et al., 2012; Koeck et al., 2014; Jamrozik et al., 2016; Pryce et al., 2016
2010s	Novel traits (including feed efficiency, milk coagulation properties, milk fatty acid contents, hoof health, and automatic milking systems) are implemented by different countries.	Ravagnolo and Misztal, 2000; Thompson-Crispi et al., 2012; Pryce et al., 2015; Chesnais et al., 2016; Lassen and Løvendahl, 2016; de Haas et al., 2017; Malchiodi et al., 2017