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Dairy Cattle Breeding

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Glossary

Allele A variant form of a gene. Differences between alleles of a gene are a result of alternate DNA sequences.

Breeding value The sum of the independent allele effects on the trait of interest (i.e., the additive genetic worth).

Generation interval The average age of the parent when he/she is replaced by their offspring.

Genome-wide selection Selection of animals based on the value of their genomic profile. Animals are genotyped for several (thousands) of markers spanning the entire genome. These markers are so

close together that they are thought to be linked with all genes in the genome.

Heritability A population measure depicting the strength of the relationship between performance and breeding value.

Indicator trait A trait genetically correlated with the trait of interest, but is easier, cheaper, or more convenient to measure and select in hopes of indirectly affecting the trait of interest in the population.

Mendelian sampling Describes the genetic variation of progeny of the same parents. More specifically, full-sibs are not expected to be genetically identical because of random segregation and recombination of genes from the sire and dam.

Reliability Regarding estimated breeding values, reliability, or accuracy of the estimated breeding value reflects the strength of the relationship between the estimated breeding value and the true breeding value.

Definition of the Subject

Dairy cattle breeding is the process of selecting and mating individuals in accordance with breeding goals, with the aim of changing genetic merit of future generations and bringing about an improvement in economic efficiency. For instance, a breeding goal may be designed to improve milk production, health, and fertility. Selection would then be for individuals who will produce offspring that genetically will earn greater profit through improved production at a lower cost (due to improved health and fertility).

Many factors have contributed to the vast improvement in dairy cattle production over the last century. One of the most important factors is the regular recording of phenotypic records. It is from these phenotypic records that the industry has estimated genetic worth. Improvement in methods for genetically evaluating dairy cattle is a large contributor to the

substantial genetic improvement seen in this species. Such methods include the use of BLUP (Best Linear Unbiased Prediction), a method first proposed by C.R. Henderson in 1949 [1]. Another important milestone in the improvement of dairy cattle breeding was the development of techniques to freeze and store bovine semen in the early 1950s [2]. Because of this, semen can be stored for longer, shipped further, and therefore shared internationally. A large contributor to the success of dairy cattle breeding has been the implementation of progeny testing programs in the 1950s, which allowed for reliable genetic evaluations for bulls, especially for traits only expressed in daughters (such as milk production) [2]. To aid in the trade and use of dairy cattle genetics on an international basis, Schaeffer in 1994 developed MACE (multiple-trait across-country evaluation) [3]. This methodology allowed genetic evaluations to be converted to different countries' scales. In 2006, Shook [4] described the remarkable increase in yield traits from 1980 to 2000, revealing an increase of 3,500 kg of milk, 130 kg of fat, and 100 kg of protein per cow per lactation. While this increase is due to improvements of many factors, including genetics, nutrition, and management, Shook [4] determined that 55% of the gains in yield traits were due to genetics and that genetic change (versus altering environmental conditions) is permanent and cumulative.

Introduction

As seen in previous entries, genetic improvement in any livestock species requires: (a) identification of breeding goals; (b) accurate data collection, animal identification, and pedigree registration; (c) breeding scheme; and (d) genetic evaluation of measured traits. In dairy cattle breeding, artificial insemination is highly used and traits of interest are usually only expressed in females. Both points determine that males are very important in breeding scheme and genetic progress, but generation interval will be longer than in other species, given that males need to be proven based on progeny performance instead of their own. Another important aspect of dairy cattle breeding is an open international market for dairy genetics, where the male side is controlled through semen sales by a large number of AI organizations, some national and some multinational based. The female side, by contrast, is

controlled by the dairy producers. Being an international market with high exchange of semen, and somewhat lower but still common exchange of embryos and live animals, a constant need is to obtain genetic values of foreign animals on local scales, a service provided via international genetic evaluations by the Interbull Centre in Sweden. Finally, in the last 2 years, the full sequence of the bovine genome has opened the way for genome-wide selection. The advent of genomic selection has provided new opportunities and challenges in the global dairy semen market. The market has already seen a partial shift from progeny tested sires to young genotyped bulls. After this transition time, provided one can confirm over the next few months that the genetic level and accuracy of evaluation of these young bulls are as high as expected, genomic selection will revolutionize dairy cattle breeding, and will decrease the importance of progeny testing for some bulls. This chapter will present all the characteristics of traditional dairy cattle breeding, the international aspects of this species breeding as well as the current application of genomic selection and its consequences.

Breeding Goals

Generally, the breeding goal of a dairy producer is to maximize the profitability of his/her dairy farm. The main return in a dairy farm derives from sales of milk production. Cost of milk varies across and within countries based on supply and demand and whether a quota system is present. Additionally, premiums are paid for high-quality milk, and higher percentages of fat and protein. Furthermore, penalization will apply for milk with somatic cell count (SCC) higher than a given threshold. The second return in a dairy farm originates from the sale of breeding stock, primarily young or pregnant heifers. This type of return is less common, being present only in dairy farms with high-genetic-value cows. The same type of farm will generate return from embryo sales by multiple flushings of their top cows. A more common but low return derives from the sale of male calves and cull cows. The most important variable cost in dairy farms is represented by feed costs, followed by veterinary and breeding costs.

For many years, most selection programs worldwide focused on increasing milk production. National selection indices were based on improving milk yield

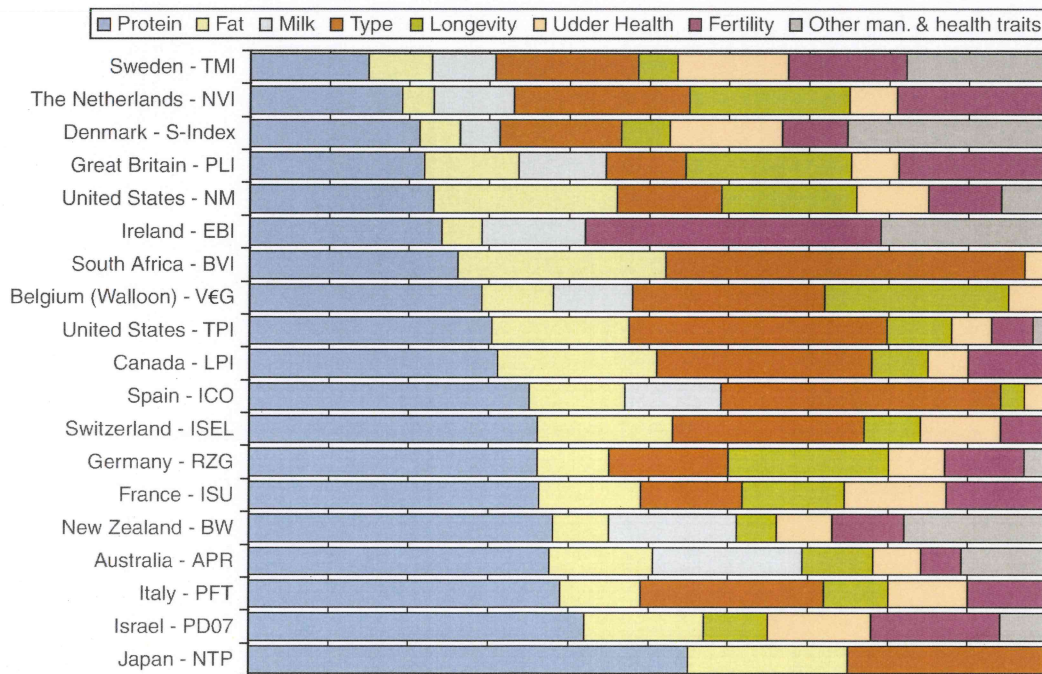
and gradually shifted toward improving protein yield and, outside North America, toward increasing fat and especially protein content. This was true for most countries with the exception of the Scandinavian countries, whose selection indices also included health and reproduction; and North American countries, whose selection indices included conformation together with production. In the last 10 years, a growing interest has broadened selection indices to include functional traits such as reproduction and health. Main reasons for this shift were quota-based milk marketing systems, price constraints, or both, together with increasing producer and consumer concerns associated with the observed deterioration of the health and reproduction of dairy cows. Labor costs have increased relatively more than milk price in some countries. Several studies have shown that selection for production alone causes negative effects on udder health [5] and reproductive performance [6–8].

Figure 1 shows the relative emphasis on traits in national selection indices in October 2009. The main difference between selection indices in various countries was the relative emphasis on production.

However, every country has now broadened their index by adding longevity, health, and reproduction to the usual production and conformation traits [9]. The search for the ideal balance between all of these important traits continues.

Data Collection, Identification, and Pedigree Registration

Proper identification, pedigree recording, and performance recording are crucial for genetic improvement of dairy cattle. Without them, accurate genetic evaluations would not be possible. In the past, animal identification was more important within the herd for management purposes [10]. However, it is now important to have proper animal identification for genetic evaluation purposes, which means that an animal's ID should be unique outside its herd. In some countries, a unique animal ID is mandatory. In the Canadian dairy cattle industry, a herd's lactation records only qualify for official publication if 80% of its first lactation animals are registered in a breed association herd book with a unique animal identification. Unique



Dairy Cattle Breeding. Figure 1

Relative emphasis of traits for various national selection indexes around the world

animal identification is not without error, however. Larger ID numbers associated with unique national or international identifications are at risk of recording errors, and ID tags can become worn-out or lost. Identification errors can also lead to inaccurate pedigree recording, though pedigree errors can occur for various reasons. Banos et al. [11] and Israel and Weller [12] showed that pedigree errors resulted in biased estimated breeding values and reduced genetic gain. Also, faulty equipment and human error can lead to inaccurate data recording. Fortunately, several techniques correct or accommodate erroneous outliers in the data (e.g., robust procedures described by Jamrozik et al. [13]).

In summary, numerous errors can occur when recording performance and pedigree information. Therefore, to ensure better quality data, it is mandatory in most countries to follow the rules and standards established by the International Committee for Animal Recording before records can be used for genetic evaluation. Several traits are of economic importance in the dairy industry, but the relative importance of each depends on the country (Fig. 1).

Test-day models are used for the genetic evaluation of dairy cattle for milk production traits in many countries. These models necessitate the regular recording of milk production traits. A good recording scheme can therefore require records for 24-h milk, fat, protein, and somatic cell count (SCC) to be taken once monthly. These are called test-day records. Generally, production traits such as milk, fat, and protein yield are moderately heritable.

While milk production traits are important, many other traits are of economic importance in dairy cattle breeding, including conformation, longevity, reproduction, health, and workability traits. Conformation (or "type") traits describe the physical attributes of the cow that are generally associated with survival, health, and reproduction. Many traits (e.g., body condition score) require visual appraisal by the recorder, and are considered to be more subjective. In these cases, it is vital that assessors are highly trained to ensure repeatable and accurate recording. Many "type" traits are moderately heritable.

Because of the negative genetic correlations between milk production and fertility or health traits, long-term selection for improved milk production has

led to reduced fertility and health in dairy cattle. As a result, routine genetic evaluations of reproductive and health traits are becoming more common, despite low heritabilities. A major challenge is that direct health data has not been recorded for very long and can be difficult to measure. In many cases, countries use indicator traits instead of measuring the health trait directly. An example of this is using somatic cell count as an indicator of mastitis.

Longevity (or survival) describes the length of a cow's survival in the herd, and has a low heritability as this trait can be greatly affected by herd management and other nongenetic factors. Workability includes traits such as milking speed and temperament during milking. Milking temperament has a low heritability, while milking speed has a moderate heritability.

Breeding Scheme

In general, a breeding scheme is the amalgamation of the processes involved in the selection and mating of livestock for the purpose of genetic improvement. Because of artificial insemination in the dairy cattle industry, semen from a single male can be used widely throughout the population. Therefore, genetic improvement is achieved largely through intense selection of males. However, most of the economically important traits in the industry (such as milk production traits) are expressed in the female. As a result, dairy cattle breeding relies on progeny testing schemes for genetic improvement. Data on various milk production and performance traits from daughters are collected and used to calculate estimated breeding values for bulls. The more daughters and daughter records are available for a bull, the greater the accuracy of the estimated breeding values. "Proven bulls" are bulls with very reliable estimated breeding values because they have many daughters with performance records. Estimated breeding values for bulls without progeny records are less reliable because they are calculated using the average of the estimated breeding values of the parents.

The major factors influencing rate of genetic progress for a given trait are the components of "the key equation" of animal breeding:

$$\frac{\Delta BV}{t} = \frac{r_{BV, BV} \hat{\sigma}_{BV}}{L} \quad (1)$$

where BV is true breeding value, t is time, \widehat{BV} = estimated breeding value, $r_{\widehat{BV}, BV}$ = accuracy of the estimated breeding value relative to the true breeding value (also the correlation between the estimated and true breeding values), i = selection intensity (a function of the proportion of the population chosen to be parents of the next generation), σ_{BV} is additive genetic standard deviation, and L is generation interval. The aim is to choose animals with superior genetics to be parents of the next generation to improve the genetics of the population. Increasing the reliability (accuracy) of prediction, selecting only the best animals as parents (increasing selection intensity), and decreasing the generation interval are important factors for increasing genetic improvement per unit time.

A major challenge in dairy cattle breeding is developing an optimum breeding program that maximizes genetic progress while minimizing cost. AI organizations are generally responsible for breeding schemes [14], and a typical AI organization can spend millions of dollars per year progeny testing bulls to find the best bull to market to the world [15]. However, dairy breeding is entering a new era in which genomic selection is possible. With genomic selection, bulls can be genotyped and selected at a young age. This improves the industry's traditional breeding scheme by reducing reliance on progeny testing (a lengthy and costly process), and will theoretically increase response to selection via a reduced generation interval [15]. Also, genomic values will increase the accuracy of genetic evaluations, especially for young sires for which traditional estimated breeding values are derived from parent averages [16].

Purebred and Crossbred Cows

The group of animals selected as parents of the next generation are expected to possess alleles that the industry considers favorable. Therefore, through selection, the frequency of favorable alleles in the population should increase with each generation while that of unfavorable alleles should decrease. The result is an increase in average breeding value, and improved performance of the dairy cattle population. The change in average breeding value over time defines the genetic trend.

As mentioned previously, artificial insemination has allowed for intense selection of sires for increased

genetic improvement over time. This means that a few top bulls, with the best collection of favorable alleles, can be mated widely throughout the population. While this is a good way to progress more quickly toward fixing favorable alleles in the population, it reduces the effective population size of the breed which could raise inbreeding and reduce performance from the associated inbreeding depression. The dairy industry needs to find a compromise between selection of the best sires for use in artificial insemination, and minimization of inbreeding depression. This is, of course, less of a problem initially with crossbreeding, as sire and dam are unrelated. However, while several benefits exist with crossbreeding in general, heterosis obtained is too low to lead to more profitable animals than purebred Holsteins (the most widely used dairy breed) [17, 18]. Therefore, in the dairy industry, selection tends to occur within breeds.

Again, a large degree of dairy cattle genetic progress is achieved through the selection and use of semen of a few top bulls. However, it is important to understand that selection and consequent genetic progress within a breed is achieved via four selection pathways, all of which center around the progeny testing scheme.

Progeny testing is required so that the genetic merit of bulls can be calculated reliably via analysis of many performance records on many daughters. Every year, genetically superior bulls and cows are mated using artificial insemination to produce young bulls with high predicted genetic merit. On average, young bulls resulting from these matings will have high true genetic merit, but because of Mendelian sampling, it is not certain that these young bulls will be genetically superior. The young bulls therefore need to be proven via progeny testing. If a young bull is in fact of high genetic merit, he will yield daughters that perform well for traits of interest. The more daughters he produces with superior performance, the more certain it is that he is a genetically superior bull.

So far, two selection pathways have been discussed: selection of sires of young bulls, and of dams of young bulls. The sires of young bulls are proven and their semen can be used widely, so they can be selected very intensely, and their estimated breeding values are very reliable. Referring to Eq. 1, increased selection pressure and reliability will lead to increased genetic progress per unit time. Dams of young bulls can be selected

intensely because not many young bulls need to be produced for progeny testing (only about 400 a year in Canada and about 6,000 Holsteins worldwide). However, the reliability of estimated breeding values for dams of young bulls is not as high as that of the sires because the dams have fewer close relatives with records.

In a dairy herd, replacement heifers are required. Therefore, further potential for increasing genetic progress of the population is through two more selection pathways: selection of sires of cows and dams of cows. It takes several years for young bulls to be fully proven. However, when these bulls have a genomic evaluation or some daughter records (but not yet enough to achieve the reliability of a proven bull), they can be selected to produce replacement heifers with a reasonably high selection intensity. Dams of these future cows, however, cannot be selected so intensely for several reasons. Many replacement heifers are required, and because a female cannot breed as many times as a male, most cows will be selected for breeding. Also, female fertility in the dairy cattle population is typically low, so the industry cannot afford to be very selective with this pathway.

Genetic Evaluation

For progress in the dairy industry, it is important to accurately select genetically superior animals as parents of the next generation. Traditionally, genetic worth could only be estimated by evaluation of phenotypic records, which are a result of a combination of genetic and environmental factors (and sometimes an interaction of the two). Again, genomics is revolutionizing the way the industry evaluates dairy cattle, making it possible to genotype animals instead of waiting for phenotypic records. However, genomics is just one part of the process, and the collection of phenotypic records will still be important for some time.

The additive genetic value of an animal for a particular trait is the sum of the independent effects of that individual's alleles on that trait. On average, half of an animal's additive genetic worth is passed on to its offspring. The greater the animal's genetic worth, the more genetically superior its offspring are expected to be. The additive genetic value is therefore appropriately termed "breeding value." Breeding values of animals

can be estimated from many different sources of information, including observations on the animal itself and observations from a variety of relatives. This reiterates the importance of quality phenotypic and pedigree data. True breeding value can never be known, only estimated from a very large (effectively infinite) number of genes with alleles each of which has a small effect on the trait of interest. Breeding values are estimated from limited phenotypic data using models that are not perfect. The accuracy of estimated breeding values (EBV) depends on a variety of factors, including the degree of relationship between the animals providing the phenotypic information and the animal being evaluated, the number of records available, and the heritability of the trait of interest. Of course, through genomics, perhaps one day the effect that each allele in the genome has on each trait could be quantified, bringing the industry closer to an animal's true breeding value for each trait.

Several traits of economic importance to the dairy industry were already discussed. So, a dairy bull or cow has several estimated breeding values, one for each trait. This makes selection complicated. For example, perhaps a potential sire has excellent estimated breeding values for milk production traits, but terrible values for health and fertility traits. Therefore, countries devise a national economic selection index, which incorporates estimated breeding values for traits of interest and their respective monetary worth into an equation that gives a single score for profitability ("aggregate breeding value") of each animal [19]. This makes selection much easier, as animals with the most favorable combination of estimated breeding values (e.g., high milk production and good health and fertility) are the most profitable.

Traditionally, selection index methods were used to combine weighting factors with adjusted phenotypic records from various sources (i.e., own records and records from various relatives) to derive estimated breeding values for traits. The phenotypic records were first adjusted for a variety of environmental influences including, for example, age of animal and effect of contemporary group. These methods of adjustment were not always effective for disentangling genetic effects from environmental influences. To improve the application of selection index methods, the dairy breeding industry began to use the statistical method

known as best linear unbiased prediction, or BLUP, in the 1970s. This method was first proposed by C.R. Henderson in 1949 [1]. Without going into too much detail, BLUP is able to simultaneously estimate environmental effects and predict breeding values while taking into account pedigree relationships.

Both the traits and the methodologies involved in national genetic evaluations vary substantially among countries [20]. Therefore, EBVs for one trait in one country may not be representative of EBVs for the same trait in another country. This makes comparing animals from different countries difficult. Dairy cattle genetics are shared internationally, especially sire genetics via artificial insemination. Therefore, the Interbull Centre was created to provide international evaluations. Specifically, the procedure carried out is called the multiple-trait across-country evaluation, or MACE [3]. This procedure allows Interbull to provide a separate list of International Genetic Evaluations to each participating country, expressed on that country's scale.

Future Directions

As previously mentioned, genome-wide selection is revolutionizing dairy cattle breeding. Young bulls benefit the most with a large increase in reliability of estimated breeding values at an earlier time in their lives, reducing the generation interval of these animals and hence increasing the speed of genetic improvement. It is fairly certain that future dairy cattle genetics research will focus on the improvement of genomic techniques.

Over the years, as quantitative geneticists improve upon techniques surrounding genome-wide selection for animal breeding, it is important to keep in mind the application of such techniques to human health. In 2008, Mardis [21] predicted that sequencing the entire human genome for \$1,000 will be feasible in the near future. While animal breeders are currently using genomics to predict the genetic value of animals for complex traits, it may one day be possible to utilize genomics to predict human individuals' genetic risk for complex, multifactorial diseases, such as Crohn's disease [22]. Research in genomics in animal breeding will certainly pave the way for research and development of genomics applied to human health.

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