

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

# Advances in breeding of dairy cattle

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# Introduction

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This collection reviews the latest research on dairy cattle genetics and advanced methods of genetic evaluation and selection. After an overview of genetic improvements achieved so far, Part 1 assesses the problem of inbreeding and genetic diversity in modern dairy cattle as well as opportunities for crossbreeding. Part 2 then goes onto review research on targeting non-production traits such as fertility, feed conversion efficiency and methane emissions as well as resistance to disease and resilience to heat stress. Part 3 then surveys the latest techniques and advances in genomic selection (GS) in such areas as functional annotation and use of sequence variants to improve genomic prediction, as well as developments in genetic evaluation (GE). The final part of the book reviews developments in embryo technologies, gene editing and the way new techniques are being integrated in practice into dairy breeding programmes.

## **Part 1 Managing genetic diversity**

Chapter 1 provides an overview of genetic and phenotypic improvements in temperate dairy systems. In the last 50 years, the dairy industry has benefitted from major advances in management, nutrition practices, reproductive technologies, and genetic selection. The refinement of selection indices over time has been shown to be an effective way to make progress on a variety of economically important traits. The chapter provides an overview of developments during this time in traits considered for selection in dairy cattle and the improvements achieved. It features sections on production and conformation initially, and the augmented with other traits such as reproduction and health. The chapter concludes with a section on other novel and functional traits as the identification and recording of additional, non-production traits (i.e. fertility) has permitted the genetic evaluation of additional, valuable traits and the broadening of selection goals. The authors note that further breakthroughs with genomic selection have enabled improvements to be made in many novel areas.

The next chapter examines assessing inbreeding and genetic diversity in the Holstein breed using pedigree and genomic approaches. Various breeding strategies to improve dairy cattle production, conformation, health and, more recently, efficiency, have been developed. However, as selection intensity within these finite populations has increased, so has the relatedness within populations. Chapter 2 looks at inbreeding and genetic diversity in the Holstein breed. It discusses the forces affecting genetic diversity within the breed, including drift, selection, migration, and mutation. Assessing measures of relatedness using different sources of information available for Holsteins

(additive genetic relationships, genomic relationships, and other measures of inbreeding) are described. Inbreeding and its effects on phenotypes, including inherited defects and inbreeding depression for quantitative traits, but also positive effects of inbreeding are then explored. Exploration of population measures of inbreeding, such as the effective population size and the rate of inbreeding leads into a discussion on how to manage genetic diversity in Holsteins. The chapter concludes with a case study on Holstein cattle in Canada.

Moving on to Chapter 3, variation between breeds in terms of genetic diversity in dairy cattle is discussed. The chapter examines domesticated cattle breeds that are selected for milk production. It reviews relevant definitions and discusses the role of natural and artificial selection in the creation of breeds and genetic diversity. The chapter then goes on to review the importance of genetic diversity both between and within breeds and provides a section on the conservation of genetic diversity in gene banks. Finally, the chapter looks ahead to future research trends in the area and provides detailed guidance for further reading on the subject.

Chapter 4 examines the use of genomic information to improve selection response while controlling inbreeding in dairy cattle breeding programs. The chapter begins by assessing population size and inbreeding, as well as reviewing how genetic information can be used to reduce inbreeding. It also provides an understanding of the genetics of inbreeding and how the construction of mating designs can be used to limit inbreeding. A section on how alleles can be maintained is also provided, and the chapter emphasises how optimum contribution selection (OCS) can be used to maximise selection response while controlling inbreeding. Finally, the chapter concludes by providing a case study of using optimum contribution selection and an overview of how genetic information can provide a new way forward in understanding and controlling inbreeding.

The final chapter of Part 1 reviews the opportunities and challenges in crossbreeding dairy cattle, specifically focusing on temperate regions. Improving performance through heterosis gained from crossbreeding has been a breeding strategy that has been used for a long time; however, when used in today's dairy systems, crossbreeding can produce profitable results for dairy producers. Interest in crossbreeding of dairy cattle has become a topic of great interest in the last ten years and has developed in response to concerns dairy producers have about fertility, calving difficulty, and stillbirths in today's genetically improved Holstein cows. Chapter 5 summarises landmark crossbreeding research at the University of Illinois before going on to consider crossbreeding research in Canada, Australia, New Zealand, the United States, Ireland and Germany. It includes a case study on crossbreeding with Jersey cows conducted at the University of Minnesota. Finally, the chapter looks ahead to future trends in this area and suggests further reading on the subject.

## Part 2 Breeding objectives and genetics of new traits

Part 2 begins with a discussion of recent developments in multi-trait selection. Selection indexes, and their underlying breeding objectives, are widely used in dairy cattle breeding, and indexes tend to play an important role in selection decisions made by commercial farmers in many of the more advanced dairy industries within well developed economies. Chapter 6 describes the key role of multi-trait indexes in dairy cattle breeding, how this role is evolving, and consequently, the methods used to establish the weightings in the indexes. Finally, the chapter looks ahead to future research trends in this area and provides guidance on further reading on the subject.

Chapter 7 examines advances in dairy cattle breeding to improve fertility/reproductive efficiency. The decline in fertility over the last few decades, especially in high milk producing dairy cows, is a major concern in many countries with modern dairy industries. Fertility is a compound trait of many events leading up to successful calving and subsequent lactation. Fertility traits in cattle have a relatively low heritability, but part of the historical decline in fertility is associated with strong selection for milk production and selection for some type traits in some dairy breeds. The chapter discusses selection approaches to improve fertility, including collection and utilization of data to carry out genetic evaluation. It reviews progress in understanding the role of genetics in addressing the decline in fertility and present, current, and future challenges and opportunities that could affect reproductive efficiency of dairy cattle. Measures of fertility and their use for genetic evaluation, and the use of different breeds and genomic data to improve reproductive performances of dairy cattle are also discussed.

The subject of Chapter 8 is advances in dairy cattle breeding to incorporate feed conversion efficiency in national genetic evaluations. The chapter begins by discussing the importance of feed efficiency as a target for breeding and goes on to review recording feed intake. Genomic selection is often cited as being particularly effective for difficult to measure and/or expensive traits since recording can be specifically organised in nucleus herds and the benefits of that recording can be distributed to others through genomic breeding values on genotyped animals that do not yet (or may never) have phenotypes. The chapter then goes on to examine the pooling of genetic data on feed intake internationally and provides a section on establishing genomic breeding values for feed efficiency. The chapter concludes by looking ahead at future research trends in this area and provides guidance for further reading on the subject.

Chapter 9 examines how using the metagenome can improve phenotypic prediction in dairy cattle breeding. New advances in metagenomics studies offer new possibilities to incorporate the metagenome information into strategies to improve feed efficiency and sustainability of animal production.

The chapter explains the importance of the microbiome in complex traits in dairy cattle. It reviews good practices and standardization of protocols in metagenomics studies and presents the most common strategies to sequence the metagenome. The chapter also discusses traditional and new metrics to measure microbial diversity and examines whole metagenome association analyses. Finally, the chapter discusses bioinformatics options to analyse the metagenome and looks ahead to future research trends in this area.

Moving on to Chapter 10, this covers advances in dairy cattle breeding to improve resistance to mastitis. Mastitis, an inflammatory response associated with bacterial infections, is generally regarded as the most-costly disease of dairy cattle because of its high incidence and effects on milk production and composition. Genetic selection for highly productive dairy cows has been very successful; however, udder health has declined in many dairy breeds because of its unfavourable correlations with milk production. Poor udder health increases veterinary and farm labour costs, increases rates of involuntary culling, decreases farm revenue, and adversely impacts animal welfare. However, genetic selection can be used to improve udder health just as it has been used to increase production. The chapter includes sections on both conventional and new phenotypes for improving resistance to clinical mastitis, and also on both national and international genetic improvement programmes for resistance to clinical mastitis. It concludes with a section on increasing rates of genetic gain through genomic selection.

Chapter 11 examines advances in dairy cattle breeding to improve resistance to claw disorders and lameness. Foot and claw disorders are, along with reproductive and udder health problems, major reasons for involuntary culling in dairy cattle. Culling due to lameness accounts for 8-15% of all culls. The chapter describes the key factors needed to achieve genetic improvement of claw health and discusses the challenges. It covers the various steps in breeding from the definition of the breeding goal, performance recording (phenotyping) with standardization and measures to improve data quality, genetic evaluation with the genetic background of traits, trait definitions, data validation and models, including aspects of genomic evaluation, direct and indirect selection for claw health and the possible impact on genetic gain. It provides examples of successful implementation into routine breeding programmes and offers recommendations and examples of best practice. Finally, the chapter looks ahead to future research trends in this area and makes suggestions for further reading on the subject.

The subject of Chapter 12 is the use of mid-infrared spectral data to predict traits for genetic selection in dairy cattle. Even in the era of genomic selection, relevant phenotypes are still needed and therefore phenotyping through the precise monitoring of the status of the cows, and their health, behaviour, and well-being as well as their environmental impact and the quality of their

products is essential. The arrival of mid-infrared (MIR) based phenotypes have made a significant impact, as they can be obtained cheaply and quickly, are usable on a large scale, and are robust and reliable. The chapter covers the state of the art, the opportunities, and also the issues that need to be addressed in order to allow the even more successful use of MIR for genetic selection of dairy cattle. The authors cover different topics from the development of MIR-based prediction equations, their specificities in modelling, and their use in animal breeding. The latest developments and opportunities related to this novel technology for genetic and genomic selection in dairy cattle are also discussed.

Moving on to Chapter 13, the chapter looks at advances in dairy cattle breeding to improve heat tolerance. Elevated temperature can impact dairy cows in many aspects, leading to a decline in productivity and ultimately the profitability of the industry. There is a need to breed for heat tolerant dairy cattle to mitigate these impacts. The chapter outlines technologies to breed for more heat tolerant dairy cattle, exploiting either between or within breed genetic variation in the trait. Finally, the chapter discusses future perspectives on the use of different tools to achieve accelerated improvements of this important trait and provides detailed guidance on further reading in this area.

The final chapter of Part 2 reviews advances in dairy cattle breeding to improve longevity. Improving longevity of dairy cows has long been of economic interest. There is also a societal interest in improving longevity and evidence suggests it is an important factor in mitigating greenhouse gases. Longevity is a complex trait to record and to improve genetically, despite considerable genetic variation being present. In most cases the farmer decides to cull a cow, and it is often for a number of reasons. Also, for animal breeders it takes too long for daughters of a bull to be culled before bull selection can take place. Chapter 14 looks at recent advances in dairy cattle breeding to improve longevity. The importance and challenges of defining a longevity phenotype are first explored followed by sections on the genetics of longevity and selection of animals before lifespan is known. Genetic evaluation and selection for longevity are then discussed. The chapter concludes with a case study on breeding of dairy cattle for productive lifespan in the Netherlands.

### **Part 3 Genetic selection and evaluation**

Chapter 15 discusses developments in genomic predictions in dairy cattle breeding by providing a historical overview of methods, technologies and applications. Selection and breeding decisions have traditionally been made based on phenotypic measurements and pedigree information of selection candidates or close relatives. However, the recent availability of genomic information on a large number of markers has transformed modern dairy cattle breeding around the world. From initial work on the identification of

Quantitative Trait Loci and candidate genes, genomic selection has developed as a genome wide approach for the selection on economically important traits, and the prediction of genetic merit of individuals for selection. In this context, several statistical methods have been developed to enable the incorporation of genomic information to achieve these goals. The chapter summarises the key developments in genomic prediction and selection in dairy cattle, with a focus on the tools and statistical methods proposed over time. Additionally, the chapter also discusses the main contributions that have supported these developments, and indicate potential constraints and opportunities in the use of current methods in the future of dairy cattle breeding.

The next chapter reviews linking to genotype to phenotype, focusing specifically on functional annotation and how it can be used as a tool to advance dairy cattle breeding. Functional annotation describes known or predicted roles of a DNA variant or DNA sequence's molecular function on the expression of a trait phenotype. Since whole-genome sequencing has become more affordable, software was developed to filter variants based on these annotations. Functional annotation can help identify causative variants, which in turn increases prediction accuracy of genomic selection, particularly across breeds and multibreed populations. The concept of integrating functional genomics information into predictive models is not new, but its application is still limited. The chapter describes how functional annotation has developed, if it is useful to dairy cattle breeders and provides examples of its uses in prediction research. The chapter also hypothesizes how functional annotation might be exploited in breeding. There is considerable hope that whole-genome gene function information may help predict phenotypes. However, considerable research is still needed to determine if functional annotation can one day play a role in dairy breeding.

Moving on to Chapter 17, this chapter examines how to find causal variants for monogenic traits in dairy cattle breeding. Many of the most striking traits we recognise in cattle are caused by one or a small number of large effect mutations. These include breed-defining characteristics such as coat colours and patterns, hair length, and horn status. Many deleterious effects in cattle can also be attributed to single genes, with phenotypic impacts ranging from mild (e.g. crop ears), to severe (embryonic lethality). The chapter summarises a range of traits impacted by major effect genes in cattle and provides examples of mutation discoveries with a focus on the methods used to identify these effects. The chapter includes analysis of emerging technologies and methods being applied to mutation discovery in cattle, examining how new molecular innovations and large-scale genomic data are playing increasingly important roles in causal gene and mutation identification.

Chapter 18 reviews the use of genomic data in large-scale genetic evaluations in dairy cattle breeding. Genomic evaluation has been successfully

implemented in nearly all advanced dairy producing countries. Methods to compute genomic evaluations for dairy cattle can be divided into single-step methods and multi-step methods. The chapter describes the use of mixed model equations and the genomic relationship matrix, as the basis of methods used to compute genomic evaluations and it explains the process of assessing accuracy and validating methods of computing genomic estimated breeding values. Finally, the chapter examines how genomic selection has changed the dairy cattle industry and looks ahead to future research trends in this area, as well as providing detailed guidance on further reading on the subject.

Expanding further on the topic of Chapter 18, the next chapter reviews international genomic evaluation methods for dairy cattle. The primary systems of data recording and genetic evaluation of dairy cattle are managed at a national level, with separate programs being run by each country, or in some cases for a small group of countries. However, international genomic evaluation methods for dairy cattle are needed as there is an intensive trade in genetic material world wide and sires can considerably re-rank in merit from one country to the next. Chapter 19 compares national versus international standards and genetic versus genomic evaluation methods. The chapter highlights key points of understanding for current and future applications of international genomic evaluation of dairy cattle. Finally, the chapter looks ahead to future research trends in this area and provides detailed guidance on further reading on the subject.

The final chapter of Part 3 examines genetic and genomic dairy cattle evaluations in developing countries. Genetic improvement programmes have delivered huge economic returns in developed countries. Supporting these successful genetic improvements are efficient genetic evaluation systems (GES) for the accurate evaluation of animals on which selection is based. Thus, GES is not only an integral and important component of any genetic improvement programme, but it has direct influence on the rate of genetic progress that is achievable. Chapter 20 discusses genetic and genomic dairy cattle evaluations in developing countries. The chapter discusses efficient data collection and storage methods covering historical perspectives, and the current status of data and data collection in some developing countries (Kenya, Zimbabwe, India and Brazil). Then follows a section on analytical systems for the computation of the genetic merit of animals covering both conventional genetic evaluation systems and genomic selection. The chapter concludes with a discussion on systems for dispersal of better genetic merit.

## **Part 4 Reproductive technologies and breeding programmes**

Part 4 begins with a discussion of developments in the use of embryo technologies in dairy cows. Reproductive technologies offer the opportunity

to produce far greater numbers of offspring from genetically valuable dams, than they would normally have in their lifetime. Technologies such as ovum-pickup when applied to harvest oocytes from prepubertal animals provide the means to dramatically reduce the genetic interval, whereas the large number of embryos recovered from multiple ovulation embryo transfer gives greater scope for selection for genetic improvement. When animal breeding programmes couple these technologies with genomic selection based on genome wide assisted selection, the accuracy of selection can be increased further. The current range of interventions that can be applied to breeding programmes provides great scope to increase the efficiency, sustainability and welfare of the dairy industry. Chapter 21 provides an update on current developments in reproductive technologies that are available for routine use and those that are still in the research stage but have the potential to provide solutions for the dairy industry in the future.

Chapter 22 reviews the use of gene editing techniques in dairy cattle breeding. As the global population increases and incomes rise, global demand for dairy products is predicted to grow rapidly. The dairy industry will need to produce more product with fewer resources in the face of an ever-changing climate. Gene editing could complement existing technologies to increase production, limit environmental impacts, and maximize animal welfare. The chapter examines applications of gene editing in dairy cattle and explains how genetic editing can be integrated into dairy cattle breeding programs. It looks at current regulations governing gene editing and provides a detailed case study based on the breeding of polled cattle. Finally, the chapter looks ahead to future research trends and provides detailed guidance on further reading.

The final chapter of the book examines the development of dairy breeding programs. Genomic selection has revolutionized dairy cattle breeding programs. Young bulls can be selected at a young age without progeny testing at a much lower cost than previously. This reduction in generation interval makes it possible to double genetic trend. Chapter 23 explains the context of dairy cattle breeding and outlines the impact of the genomic revolution on breeding dairy cattle. It looks at new breeding objectives and genetic trends, genomic selection and genetic diversity, the impact of female genotyping and selection for new traits. Finally, the chapter looks ahead to future research trends in this area and provides guidance on further reading in this area.

# Part 1

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## **Managing genetic diversity**

# Chapter 1

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## **Genetic and phenotypic improvements in temperate dairy systems: an overview**

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### **1 Introduction**

Genetic selection of dairy cattle has helped to forge the industry into what it is today. The array of traits targeted for improvement has expanded and evolved over time as a response to the dynamic requirements of producers, consumers and society, facilitated by advances in technology and trait-recording programmes. Fifty years ago, selection concentrated almost solely on increased production with consideration also for idealized animal conformation. Milk sales represented the major source of revenue for a dairy producer, and therefore, herd economics helped concentrate selection goals on increasing fat and protein production for many decades.

Milk-recording programmes have permitted large amounts of data to be collected for use in genetic evaluations, allowing large gains in production to be achieved. Concurrently, recording and consideration of cow conformation were important to continue breed standards and realize success in judged competitions and sales while also improving functional conformation. The need to identify new traits and acknowledge additional areas for genetic improvement came in part from noticed genetic decline in other important

traits, such as fertility and health, following the strong unaccompanied selection for production alone. This led to the emergence of expanded, more balanced breeding goals which included previously unappreciated non-yield traits that help to improve economic efficiency by reducing costs rather than by increasing product output.

The ability to select for and improve various traits relies on the recording and access to clearly defined, accurate and cost-effective phenotypes. The amount of data collected throughout the production chain has increased dramatically over time, giving rise to new phenotypes to be used in the selection for functional traits, either directly or indirectly, which was not previously conceivable. For many functional and novel traits, the recording of relevant phenotypes had been a limiting factor for their inclusion earlier in breeding goals, and this remains a challenge to overcome for many desired traits. A further obstacle in the genetic improvement of many traits has been the large environmental effect on the phenotypes leading to low heritability estimates. Advancing technologies available to genetic evaluations, the most impactful being the introduction of genomics, have allowed selection to happen on such lowly heritable traits where large-scale recording is difficult.

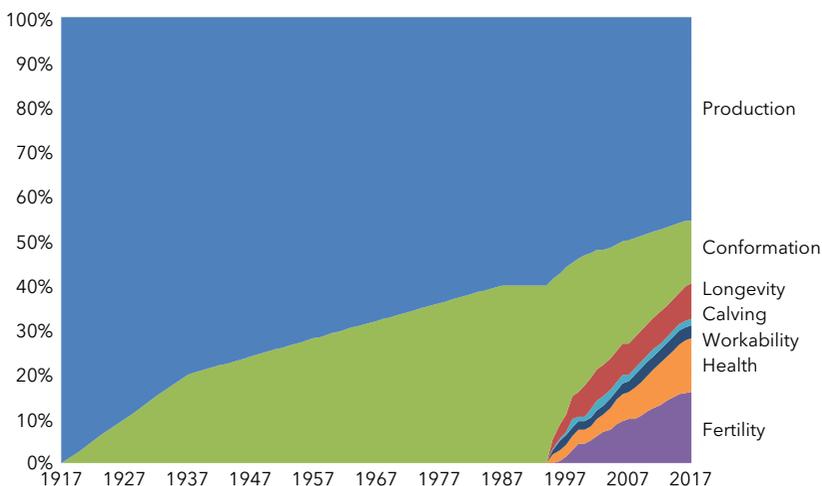
The dairy cattle industry has observed substantial changes in the number and scope of the various traits selected for in recent years. This has been a reflection of both the shifting needs of the industry and society and advancements in technology and data recording. As the number of traits genetic programmes are interested in and capable of performing genetic evaluations for keeps increasing, selection goals must continue to broaden and ultimately need to be balanced in order to proceed to improve the overall efficiency of the industry. This chapter provides an overview of developments over the last fifty years for traits considered for selection in dairy cattle and the improvements achieved.

## **2 Production**

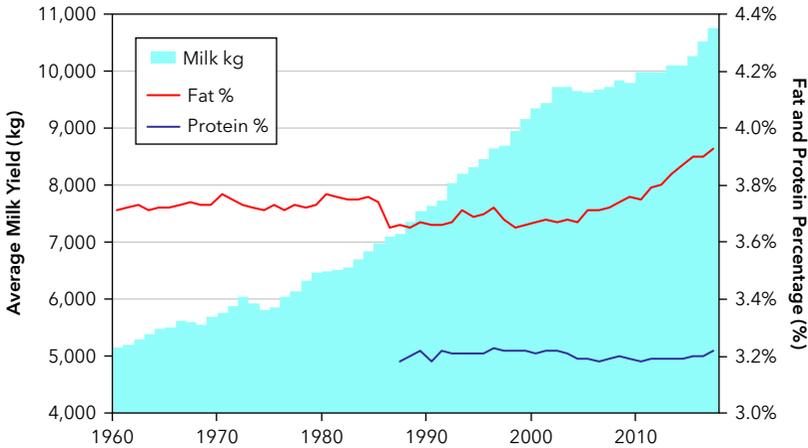
A fundamental goal in dairy cattle breeding has long been the selection for increased production. The vast majority of revenue is generated from milk sales, and thus, cows with greater milk yields were sought to maximize the profit of the dairy industry. Selection for increased production was aided by the widespread adoption of milk performance testing in the early 1900s with the recording of milk weights, the analysis of butterfat, and later, solids-not-fat contents. Dairy Herd Improvement Association (DHIA) testing was commonplace, generating large numbers of records for production traits to be used in genetic evaluations to identify superior families and individuals, particularly important in the AI industry. In the 1970s, milk protein testing became readily available with the introduction of mid-infrared (MIR) methods into milk-recording programmes.

Infrared analysis of milk samples provided rapid and less expensive measures of fat, protein and lactose than those previously available (Biggs, 1972). Premiums were paid by milk processors for fat and protein contents, giving the milk components economic value and targeting their improvement in genetic selection programmes.

The dependency of overall income on milk and component yields, paired with the ease and prevalence of their routine recording, rationalized the dominance of the production component in selection indices (Fig. 1). A further encouragement for the selection of production traits was that success through breeding was readily achieved and observed for these traits. Fortuitously, milk, fat and protein yields have moderate heritability estimates, with ranges of 0.20–0.55, 0.14–0.52 and 0.18–0.51, respectively (Interbull, 2018). Body conformation traits, the second category contributing to early genetic selection indices, were sometimes selected for the purpose of exploiting their perceived relationship with production traits. Some early investigations found positive genetic correlations between yield traits and dairy character, angularity and udder depth (O'Bleness et al., 1960; Brotherstone, 1994). However, the use of body conformation traits for selection for increased production yielded marginal gains when compared to the use of production records alone. Strong selection pressure for increased production in the past, along with improved management considerations, has generated large phenotypic gains as demonstrated by the milk production of the average Holstein cow in Canada increasing from 5150 kg in 1960 to 10750 kg in 2017 (Fig. 2; Canadian Dairy Information Centre, 2018).



**Figure 1** Schematic representation of relative emphasis of traits included in an average selection index over time. Source: adapted from Miglior et al. (2017).



**Figure 2** Phenotypic trend of average milk yield (kg), fat and protein percentage in Canadian Holstein cows by birth year (from 1960 to 2016).

Geneticists initially utilized standardized accumulated 305-day lactation yields of cows estimated from monthly test-day information collected by milk-recording organizations in their evaluations. The methodologies for the genetic analyses developed over time and with computing advancements. For production traits, the introduction of the test-day model, where individual test-day records relative to herd mates on a given test date are modelled, was one such progression (Weigel et al., 2017). The employment of test-day records also permitted the possibility for the evaluation of persistency of production (Jamrozik et al., 1997). With the advent of genomic selection, many new methodologies appeared and granted more reliable evaluations for young bulls, without having to wait for progeny-testing schemes (VanRaden et al., 2009). As a result, the rate of genetic improvement for yield traits could be accelerated, and even larger gains in production traits were achieved (Weller et al., 2017).

For decades, the focus of selection programmes on improving milk and component production with little consideration of functional traits has revealed antagonistic relationships between high production and health and fertility of dairy cattle. Unfavourable genetic correlations have been reported between milk yield and mastitis (Simianer et al., 1991; Pöso and Mantysaari, 1996), milk component traits and metabolic diseases (Simianer et al., 1991; Koeck et al., 2013), and milk yield and fertility traits (Pryce et al., 1997; Dematawewa and Berger, 1998; Roxström et al., 2001). Physiological mechanisms for the decline in fertility are not known, but genetics along with the inappropriate nutrient management of high-producing dairy could contribute to sub-fertility (Pryce et al., 2004; Leblanc, 2010). Increased awareness and the desire to improve

reproduction, health, general well-being and welfare of dairy cattle have taken some of the emphasis away from production traits to develop more balanced selection goals.

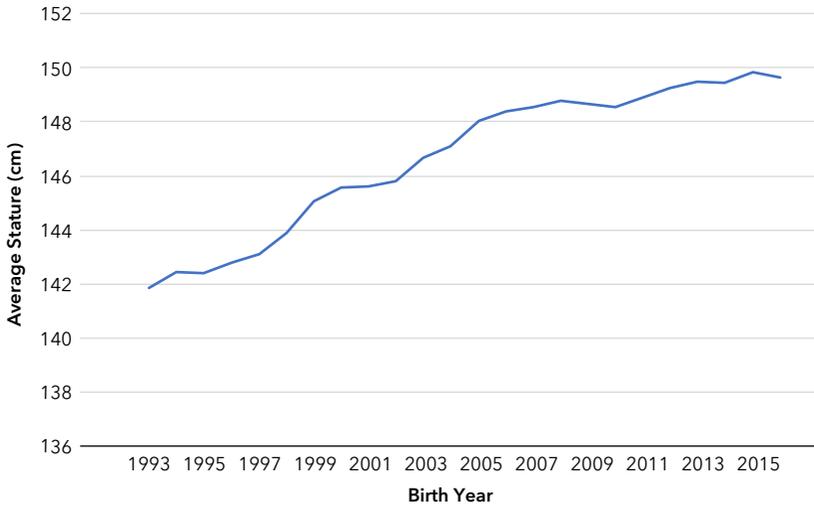
### 3 Conformation

Conformation traits, or type traits, such as udder depth, placement of teats, foot angle and stature, have been of interest to breeders since the beginning of the genetic evaluations in dairy cattle (Thompson et al., 1983). These traits are very important for breeders and farmers due to their association with functional traits (i.e. longevity; Schneider et al., 2003) and also have a direct influence on culling decisions. Conformation traits have been widely used as indirect selection criteria for longevity in dairy cattle (Larroque and Ducrocq, 2001).

The classification system based on four scorecards (i.e. general appearance, dairy character, body capacity and mammary system) was introduced in 1929, recorded only for registered cows by the Holstein-Friesian Association in the United States (White, 1974). In 1981, linear-type traits were implemented using mixed model methodology considering scores on a linear scale to evaluate both registered and non-registered cows (Thompson et al., 1981). Even though most conformation traits are considered visual appraisal, linear traits are expressed on a scale (i.e. 1-9 or 1-50 points), allowing to identify a cow with the desirable conformation trait based on its biological continuous scale. The four major categories on the classification scorecard are udder conformation, feet and legs, dairy strength (thoracic and abdominal body conformation) and rump (rump angle, pin width, loin strength and thurl placement).

Traits related to size, such as stature, are linked to body weight, which is fundamental to regulate feed efficiency and energy balance. The intense genetic selection over the years for milk production resulted in a correlated response in conformation traits, generating taller, wider and deeper animals and changes in the teat placement (Berry et al., 2004). The changes in conformation may be associated with cow health, for example teat length and position could increase susceptibility to mastitis (Lund et al., 1994; Van Dorp et al., 1998; Sewalem et al., 2004) and low foot angle, and wide rumps have been associated with lameness (Boettcher et al., 1998). In terms of the stature, the average height of Canadian Holstein cows increased (0.28 cm/year) from 1993 to 2016 (Fig. 3). Stature has a strong correlation with calving ease, as larger calves typically lead to difficult births (CDN, 2016).

Conformation traits have shown a high influence of genes of additive action, with heritability estimates ranging from 0.05 (foot angle) to 0.70 (stature) (Interbull, 2018). Most countries have included conformation traits in their national selection indices, considering different weights and composites of the traits according to their breeding goals (Miglior et al., 2005; VanRaden



**Figure 3** Phenotypic trend of average stature (cm) in Canadian Holstein cows at 26 months of age per birth year (from 1993 to 2015).

et al., 2018). The United States has included in their national Net Merit Index a composite trait for feet and legs (stature, rear legs, foot angle, feet and legs score) and body size (stature, strength, body depth, dairy form and rump width) with the percentage relative economic weight equal to 2.7 and  $-5.3$  (VanRaden et al., 2018). In Canada, a durability component is considered in the Lifetime Performance Index (LPI) including the traits herd life, mammary system, feet and legs, and dairy strength with a relative weight from 30% to 40%. The average Canadian herd considering animals born from 2011–2015 has achieved 0.8 estimated breeding value points annually in terms of LPI of genetic progress for conformation (Canadian Dairy Network, 2015).

Genomic evaluations have carried a considerable improvement for conformation traits in dairy cattle in terms of reliability gain compared to the traditional value (from 19.4% to 45.5%) (Wiggans et al., 2017). Selection for conformation traits is essential to improve longevity, health and fertility traits, thereby achieving a profitable herd in the dairy industry. The reliability of these traits has increased with the genomic evaluations and combining data of the different countries and new phenotypes.

## 4 Reproduction

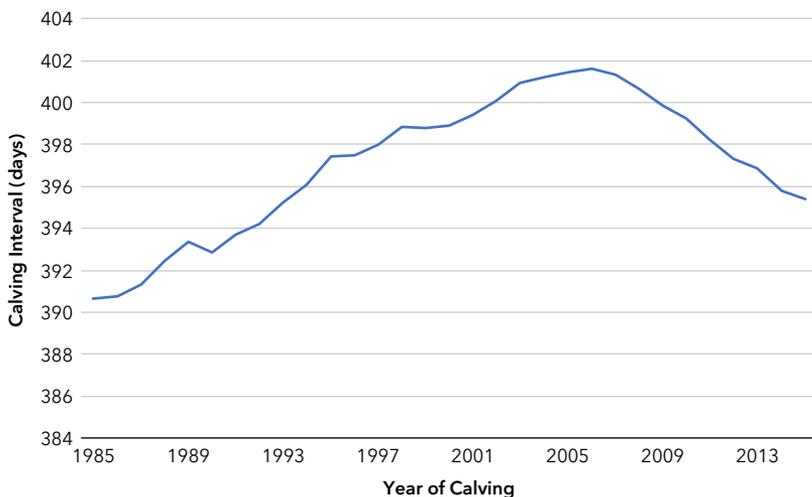
Female fertility in dairy cattle has been given most of the attention in genetic selection for reproduction, despite the fact that different fertility measures in dairy breeding can be affected by either the cow or the bull. In order to maximize

milk production and reduce management requirements, it is fundamental that a heifer or a cow successfully establish pregnancy in a timely manner.

Even if it has been long suggested that the reproductive efficiency of the cow is an important factor in determining the mean reproductive efficiency of its offspring, the possibility to select for reproduction efficiency has been often questioned because of the very low heritability estimates reported for most of the fertility traits (from 0.01 to 0.10; Interbull, 2018). The large residual variation observed for fertility traits is possibly due to not only the large impact of environment and management on these traits but also the low quality of the data.

Despite the fundamental role that reproduction plays in the productive life of an animal, reproductive measures in the general indices were introduced relatively late, mostly due to lack of data (Fig. 1). In the late 1970s, Nordic countries started to include reproduction traits in their national selection indices. They remained the only countries to consider these traits for many years. It was only later that more countries, including several European countries, Australia, New Zealand and the United States, started incorporating fertility in their national selection indices (Miglior et al., 2005). Including reproduction traits in the general index helped to slow the decline observed in cow fertility, which was partially due to the antagonistic correlations of female fertility with milk production and the consistent selection for higher yields in dairy cattle (Pryce et al., 2004). In general, the phenotypic trend observed for calving interval showed slowing deterioration in the 2000s compared to the 1990s, with some countries displaying a switch to favourable trends in this time period (Pryce et al., 2014). In Canadian Holstein cows, the calving interval between first and second calving has decreased over the last 10 years (Fig. 4). In Canada, the total realized genetic gain for daughter fertility between 2004 and 2009 was  $-0.72$  Relative Breeding Value points (RBV have been standardized to average equal to 100 with a standard deviation of 5 for proven sires), which reversed to  $1.06$  RBV points of genetic gain between 2011 and 2016 (Canadian Dairy Network, 2017). In order to realize further progress in this area, improving the understanding of genetic components of fertility is imperative.

When referring to reproduction, the fact that a cow successfully achieves pregnancy is not the only important aspect. It is key that once established, the pregnancy terminates successfully, ideally leaving a healthy cow and a viable calf without human intervention. Differentiating between cows failing to establish pregnancy and those not maintaining pregnancy may be important for improving these two different aspects that lead to reduced fertility and increased calving intervals. Moreover, when a cow concludes a full-term pregnancy successfully, problems during calving can still occur. A significant proportion of births are assisted to a major degree and could yield a stillborn calf (Meijering, 1984). Between 1985 and the late 1990s, several countries reported increasing stillbirth rates for Holstein cattle (Meyer et al., 2001; Steinbock et al.,



**Figure 4** Phenotypic trend of the calving interval from first to second calving in days considering the last 50 years for Holstein cows in Canada per year of calving (from 1985 to 2013).

2003; Hansen et al., 2004). The selection focused on early maturing cows may have contributed to accentuated problems related to calving, as young animals calve for the first time often before reaching their mature size. Both calving difficulty and calf mortality represent major problems affecting the profitability of dairy farming. The eventual death of the calf can be very costly, especially if the dead calf is a female.

Additionally, problems occurred at calving can lead to decreases in both productive and reproductive performance of the animal (Dematawewa and Berger, 1998). When analysing calving ease, two factors should be considered: direct calving ease, which is related to the calf, and maternal calving ease, which expresses how easy the cow gives birth. As with other fertility traits, calving performance and stillbirth were first considered in the national indices by Nordic countries (Philipsson et al., 1994). Genetic evaluations for calving ease traits, however, were also available early in other countries, such as the evaluation of service sire calving ease, which has been published in the United States since 1978 (Shook, 2006), and sire evaluations for calving ease published in Canada in 1981 (Cady and Burnside, 1982).

## 5 Health

Disease in dairy cattle is a serious cause of economic loss in the dairy industry as a result of reduced production, death, premature culling of animals, veterinary treatments, lost milk due to antibiotic use, added labour, delayed conception,

reduced genetic gains, low milk quality and increased susceptibility to other diseases. Further to the economic importance, the noted declining genetic trend for health and appreciation of animal welfare and antibiotic resistance concerns stressed the need to explore genetic selection for improved health in dairy cattle breeding programmes. Although a deserving trait for selection, consideration of health traits has been arduous due to the difficulty in obtaining sufficient accurate, standardized records, along with the commonly low heritability of health traits.

The first significant means for selecting for improved health appeared with the recording of somatic cell counts in many milk-recording programmes in North America and Europe in the late 1970s. Somatic cell count, log-transformed to somatic cell score, was easily recordable, moderately heritable, and associated with clinical and subclinical forms of mastitis, the most prominent and economically significant disease impacting the dairy industry. Many national evaluations for udder health concentrate on somatic cell score, which has heritability estimates in the range of 0.08–0.30 (Interbull, 2018). Additional traits evaluated for udder health include various conformation traits, milking speed and clinical mastitis (Miglior et al., 2005).

Easy to measure, heritable indicator traits were similarly sought for other prevalent clinical and subclinical disorders such as ketosis (Pryce et al., 2016). Milk  $\beta$ -hydroxybutyrate (BHB) content is an attractive indicator trait as it can be estimated during milk recording. Heritability estimates 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).

National systems for health data recording providing records for genetic evaluations were established in the 1970s for Nordic countries, which was achievable in part because only veterinarians are allowed to treat animals in these countries and those treatments are recorded by law. Later, some countries (e.g. the United States and Canada) without regulated health-recording systems began collecting producer-recorded health events to be used in genetic evaluations (Zwald et al., 2004; Koeck et al., 2012). A large number of disease traits are recorded, the most prevalent being mastitis and ketosis. Generally, low heritability estimates (0.02–0.10) have been reported for the incidence of various clinical health disorders, but the observed genetic variation is 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; Koeck et al., 2012). The recording of hoof lesions in the dairy cow population has brought another important group of health-related traits, which have heritability estimates ranging from 0.01 to 0.13 (Koenig et al., 2005; Van der Spek et al., 2013; Malchiodi et al., 2017). Some countries, such as the Netherlands and Canada, have recently implemented genomic evaluations for hoof health traits.

Clinical health data and various indicators of health are now used in genetic evaluations, and health makes up a component of many national breeding objectives to balance selection for production and promote improved health (Miglior et al., 2017). The occurrence of individual maladies has a strong environmental component leading to low heritability, and selection may not produce overt results quickly. Genomic selection could help to achieve more reliable breeding values for health traits. It is still crucial to have accurate health records on a large proportion of the population to contribute to evaluations.

## **6 Other novel and functional traits**

Cow longevity is a key trait which defines the ability of or length of time a cow remains in the productive herd and is directly associated with the profitability of dairy production systems (Allaire and Gibson, 1992). Over time, different measures of longevity have been proposed, including age at disposal or last calving, number of lactations, survival to a fixed age or lactation number and longevity adjusted for milk yield. Selection for longevity incorporates the improvement of many different components that cover the vast number of reasons for the culling of an animal. Indicator traits for longevity were attractive because to attain a completed record for longevity, a cow or daughter of a sire must have reached the end of their productive or another decided time point. Such indicator traits include production, somatic cell score, milking speed, non-return rate, interval from calving to first service and certain conformation traits (Cruickshank et al., 2002; Sewalem et al., 2007). Many countries currently include measures of direct and/or indirect longevity in their genetic evaluations (Miglior et al., 2005), although there is great variation in the longevity trait definition and the methodology used in the evaluation. Heritability estimates reported by various countries range from 0.02 to 0.22 for their longevity evaluations (Interbull, 2018). The integration of genomics into evaluations may be advantageous for longevity evaluations because it eliminates the need for a long length of time to receive an actual record to get a reliable direct longevity breeding value, so less importance can be put on indirect measures. Furthermore, advances in the selection for the individual traits that promote a long-lasting cow in the herd can serve to improve cow longevity.

Workability traits, defined as traits that facilitate working with cows on the farm, have also become more important over the past decades, especially with an increase in use of automated milking systems (Chesnaix et al., 2016). The most important ones are milking temperament (or more generally, behaviour) and milking speed, as they have economic impacts on the production system (Schutz and Pajor, 2001). Several measures of milking speed have been proposed over time, including peak flow, duration of peak rate, average flow, per cent of milk produced in the first 2 min of machine milking, the amount

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