Invited review: Academic and applied approach to evaluating longevity in dairy cows

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ABSTRACT

In its simplest form, longevity is defined as the ability to live a long life. Within the dairy industry, longevity has been defined and measured in many different ways, and the aim of this review is to disentangle the definitions and provide some clarity. Using a more standardized approach for defining and measuring longevity, both in academic discussions and on-farm application, we suggest using herd life (days) for time from birth until culling, and length of productive life (days) for time from first calving until culling. Despite identified benefits of extending the length of productive life, global trends in the time spent by dairy cattle in the herd have mostly been negative. Factors influencing herd life, such as health, rearing, environmental conditions, and management, are often ignored when longevity goals are evaluated, thereby underestimating the effect these factors have on defining overall longevity. Also, production efficiency, herd profitability, and welfare are not necessarily served by the longest life but rather by the optimized length of herd life instead. The majority of research has focused on the role of genetics on longevity. In this review, we provide insight into influences affecting dairy cow herd life as well as farm- and cow-level factors associated herewith. Finally, we suggest using herd life, including reproduction, production, health, and youngstock performance, for farm-level evaluation and length of productive life for time spent in the lactating herd.

Key words: herd life, culling, replacement, economics, productive life

INTRODUCTION

Since the start of the 21st century, the decreasing average time a cow stays in the herd (as reflected by age at culling) has been of growing concern for dairy industries across the globe (Rushen and de Passillé, 2013). In the absence of human intervention, a dairy cow is biologically capable of a life span of up to 20 yr (Nowak and Walker, 1999), yet average time in the herd currently ranges between 4.5 and 5.5 yr, or 2.5 and 3.5 lactations (Wathes et al., 2008; Knaus, 2009).

Human intervention is often cited as the cause of a reduced length of life due to the seemingly “unnatural” housing and management conditions of some dairy systems and an almost exclusive focus on genetic selection for production-related traits before the 1980s (Fraser, 2008; Knaus, 2009; Oltenacu and Broom, 2010; Egger-Danner et al., 2015). Extensive research focusing on genetic, environmental, and management factors affecting time in the herd has been conducted in attempts to increase understanding and guide farm profitability. However, the amount of time cows spend in the herd is still much shorter than their biological capability (Council on Dairy Cattle Breeding, 2019).

More efficient production leads to economic, environmental, and animal welfare benefits and often is associated with a longer productive life, often referred to as longevity. Therefore, the dairy industry has strived to increase longevity (Essl, 1998; Hadley et al., 2006; Bell et al., 2011; Rushen and de Passillé, 2013). Based on available data, dairy cow longevity, referred to as both herd life (**HL**; from birth until culling) and length of productive life (**LPL**; from first calving to culling), has generally decreased, where culling is referred to as a dairy cow leaving the herd regardless of reason, destination, and condition at departure. The aim of this review, therefore, was to explore current understanding regarding longevity, HL or LPL, to identify factors affecting HL and LPL, and to identify knowledge gaps where further understanding is needed.

Received June 7, 2020.

Accepted August 10, 2020.

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Table 1. Terminology and definitions for longevity in the scientific literature

Term	Definition	Source
Length of productive life	Days between first calving and culling or death Number of months in milk between first calving and 84 mo of age Days from one calving to the next calving, death, or culling	Compton et al. (2017) Caraviello et al. (2004) Sewalem et al. (2005a)
Herd life	Time between birth and last test day Days from first calving to culling Days from first to last calving	Vollema and Groen (1996) Brickell and Wathes (2011) Gill and Allaire (1976)
Productive herd life	Length of time that individual cows remain in herds after their first calving Days from date of first calving to date of culling or last dry date	Hare et al. (2006) Jairath et al. (1995)
Stayability	Stayability until 36, 48, 60, or 72 mo of age and stayability until 12, 24, 36, or 48 mo after first calving Proportion of cows still alive at 48 mo of age Capability of an animal to remain in its herd over time Measurement of the fraction of animals still alive at a particular age within an opportunity group	Vollema and Groen (1996) Oltenacu and Broom (2010) Essl (1998) Essl (1998)
True stayability	The ability to delay culling	Ducrocq (1987)
Functional stayability	The ability to delay involuntary culling	Ducrocq (1987)
Functional longevity	The ability to delay involuntary culling Days from first calving to culling, death, or censoring; adjusted for the effect of milk yield Longevity corrected for milk yield relative to the herd mean	Beaudeau et al. (1995) Sewalem et al. (2008) Heise et al. (2016)
True longevity	Longevity as actually observed	Beaudeau et al. (1995)

CURRENT UNDERSTANDING OF LONGEVITY

Understanding the Current Terminology for Longevity

The term “longevity” describes a long existence or length of life (Simpson and Weiner, 1989). In dairy cattle, longevity has been referred to as the time that commercially producing cows, rather than retired or pet cows, remain in the herd (Alvåsen et al., 2018). Life in cows is complex and many factors contribute to determining a cow’s true LPL, including intrinsic (milk yield, health, reproductive status, and reproductive performance) and extrinsic (milk price, salvage value, cost and availability of replacements; Bascom and Young, 1998; De Vries, 2013) factors, making it difficult to develop herd-specific long-term goals for LPL. Consequently, many different definitions and methods of measuring longevity have been developed (Table 1). Longevity has been measured as age at last calving, number of lactations, length of life between first calving and culling, age at culling or removal, and survival to different ages (Van Doormaal et al., 1985). In research, economic evaluations of longevity tend to measure lifetime productivity or cost per day of life (De Vries, 2020), whereas studies focusing on genetic, environmental, or managerial factors associated with longevity have used either a stayability or a lifetime

measure of longevity, such as HL or LPL (Ducrocq et al., 1988a).

Stayability refers to a cow’s ability to remain in the herd over time by avoiding being culled and typically evaluates whether a cow has remained in the herd until a specific point in time (e.g., to a specific age, parity, or production level; Ducrocq et al., 1988a). This approach is best suited for studies in which it is impractical or unnecessary to follow subjects to their end point—for example, analyzing the effect of calfhood risk factors on survival to first calving. However, a disadvantage to this approach is that cows culled 1 d or 1 yr before the set time point (e.g., first calving) result in an equal estimate for stayability, with variation in range of survival time being unaccounted for (Ducrocq et al., 1988a). This is avoided in definitions taking (daily) time steps into account.

Lifetime measures treat longevity as a continuous variable and are most often analyzed using Weibull survival models, based on work by Ducrocq et al. (1988a). This allows for the inclusion of “incomplete” (i.e., cows are still alive) records in the analysis and is now fundamental to measuring cow longevity in research (Weigel et al., 2017). Subsequently, LPL has become the most common approach to defining longevity, with some studies making slight adjustments to how the outcome is measured based on their specific objectives.

Terms such as “functional longevity,” “herd life,” “productive herd life,” and “length of productive life” all refer to some measure of how long cows stay in the lactating herd and have therefore become synonymous with the term “longevity.” The term “productive life span,” on the other hand, recognizes that life is cut short through human intervention, and it has been proposed that the term “longevity” be reserved for natural length of life (De Vries and Marcondes, 2020). Differences are mainly based on inclusion of the rearing period or end point based on lactation number or day leaving the herd. However, the variability in terms has led to multiple terms defining a single trait or the same term defining multiple traits (Table 1). For example, both LPL and HL are used to define the number of days between first calving and culling (Beaudeau et al., 1995; Hultgren and Svensson, 2009; Brickell and Wathes, 2011), whereas HL is also used to define the time between birth and culling (Vollema and Groen, 1996; Table 1). To further confuse the issue, authors sometimes use different terminology interchangeably within a single paper or fail to clearly define the context in which a term is being used. Similarly, if all terms are used interchangeably and synonymously with the term “longevity,” it becomes unclear whether longevity in dairy cattle refers to total life span, productive life span, or simply the ability to survive to a certain point.

Finally, livability is the ability to not die or be killed on the farm (VanRaden et al., 2018). Cows that die on the farm generate no beef income and may have more health expenses than cows that are culled (VanRaden et al., 2018). In the United States, the genetic merit of livability is a measure of the cow’s ability to stay alive while on the farm. Thus, animals that are expected to have the same productive life may have different expected end-of-life incomes depending on their genetic merit for livability.

Recommended Terminology and Calculations for Longevity

The primary purpose of studying longevity has been to develop best management and genetic selection strategies to increase longevity based on a clearer understanding of how the aforementioned factors affect longevity. It is difficult, therefore, to suggest a single definition for longevity for the purpose of academic discussions, as the outcome of interest varies among studies, as was identified by Fetrow et al. (2006) for the definition of culling. It is, however, feasible to standardize the terminology used. The following are recommendations for defining and calculating specific measures of longevity.

LPL. Length of productive life, presented by Ducrocq et al. (1988a), should be used only in reference to the length of time in the lactating herd, calculated as the number of days between first calving and culling or death. Any modifications to this description should be incorporated into the terminology used when defining the outcome. For example, we propose defining the measurement of LPL on a lactational basis (i.e., time to next calving, culling, or death) as lactational productive life (Table 1).

HL. Herd life, as described by Brickell and Wathes (2011), should be used when referring to the entire time an animal spends in the herd, rather than time in the lactating herd, and should be measured as the number of days between birth and culling or death. If an author is referring to productive HL, we propose using LPL or productive life (Table 1).

Stayability. Currently, the term “stayability” is used to describe 2 distinct definitions of longevity: the ability to avoid culling, and the proportion of cows surviving to a specific point in time. These 2 definitions are, however, related; the first refers to what is being measured and the second describes how it is measured. Multiple definitions for a single term, however, create confusion, and a method for distinguishing between these definitions is needed. Therefore, when referring to a cow’s ability to avoid culling, the term “stayability” should be used (Essl, 1998). However, when referring to the ability to remain in the herd to a specific point in time, the term “survivability” should be used instead (Table 1).

Survivability. Henceforth, the term “survivability” should be used to describe the proportion of cows surviving to a specific point in time and should be calculated as the number of cows that have survived to a given point in time divided by the number of cows included in the opportunity group. Additionally, the point of time of interest should be included in the definition (e.g., survivability to 48 mo of age or survivability to 12 mo of productive life).

On-Farm Application of Longevity. At the farm level, herd statistics such as turnover rate, average parity, average age at culling, or percentage of the herd in third or higher lactation are commonly used by producers and DHI associations to measure and benchmark HL- or LPL-related culling in their herds (Fetrow et al., 2006; Lactanet, 2019a). A cow’s longevity is determined by culling decisions made by the producer based on a multitude of factors. Traditionally, culling has been classified as voluntary or involuntary. Culling is voluntary when cows are culled due to low production and no known disease exists or when excess cows are sold for dairy purposes. Culling is defined as involuntary when cows that would have been kept otherwise are culled

due to death, disease, or reproductive failure (Gröhn et al., 2003). Alternatively, a clearer classification is based on forced and economic reasons for culling, where forced culls are cows for which no possible productive future exists and economic culls are cows for which it is economically sensible to replace them with another cow (Fetrow et al., 2006). This can occur if new heifers become available to replace an existing older dairy cow. Regardless, most culling decisions occur before cows have reached their maximum performance capacity, primarily due to the occurrence of health disorders (Beaudeau et al., 2000). Specifically, reproductive failure, teat and udder health, and feet and leg problems are the most common reasons for premature, forced culling (Bascom and Young, 1998; Doornewaard et al., 2018; Canadian Dairy Information Centre, 2019a). Producers, therefore, use HL- or LPL-related measures as an indicator of their farm-specific ability to successfully raise healthy, productive, reproductively successful cows (Lactanet, 2019b).

A point of concern is that the measures used to represent on-farm longevity fail to include any indicators related to management or cow performance and are instead simply a representation of the average time cows spend in the herd. Further, common terminology refers to cow-level longevity, yet evaluating this measure is using it as a herd-level statistic. Additionally, looking solely at herd statistics without consideration of the productive, reproductive, health, or economic conditions of the herd under which these statistics were achieved can lead to serious misjudgments regarding performance (Fetrow et al., 2006). For example, longer longevity may represent problems in the herd, such as poor reproductive performance, resulting in open cows being continuously inseminated late into lactation or an inability to successfully rear replacements (De Vries, 2017). Producers, therefore, keep older, less productive cows solely for their ability to conceive and continue producing due to a lack of available internal replacements. Similarly, a shorter longevity could represent a successful producer who has an excess of replacement heifers and believes in the value of a younger herd, and therefore sells older cows for dairy purposes. Further, none of the presented parameters reflect factors such as milk price, which affects longevity and culling decisions.

With dairy farming being a dynamic and integrated production system, decision making to optimize management and farm profitability is complex (Cabrera, 2018). The effect of income maximization per unit of physical output in dairy production (e.g., milk) is often the focus over maximization of production per cow (Houben, 1995). Criteria for economic optimization of HL or LPL will vary across the globe because, in theory, optimizing occurs through focusing on the

most limiting factor. For the United States that can be profit per cow per day, whereas in Canada under a quota system the focus would be profit per kilogram of fat. In Canada, the most comprehensive measure of longevity used by producers is profit in CAD per day of life, which is calculated to include youngstock rearing costs, quota ownership costs, overhead costs of production, and production revenues to date (Lactanet, 2019c). Many economically important factors, such as health and reproductive performance, are excluded from this calculation. However, the significance of economically important factors has been recognized in other evaluations of lifetime profitability focusing on breeding values, such as Pro\$, a profit-based Canadian national selection index calculated by weighting the profit response of certain traits based on their economic significance to producers (Van Doormaal et al., 2015; Canadian Dairy Network, 2019a). Traits incorporated into the Pro\$ calculation include milk yield, SCS, daughter fertility, BCS, calving ability, and type traits for mammary functionality, feet and legs, dairy strength, and rump as major scorecard type traits (Van Doormaal et al., 2015). Similar in the United States are the lifetime net merit index and its predecessors, which first included only milk and fat yield in 1971. The lifetime net merit index is amended regularly (last in 2018) and now includes a total of 13 traits and composites, including a health trait subindex consisting of mastitis, ketosis, retained placenta, metritis, displaced abomasum, and milk fever (Cole and VanRaden, 2018; VanRaden et al., 2018). Inclusion of health and reproduction traits in these economic-based selection indices demonstrates the economically important role they play in determining herd profitability. Structural changes to the lifetime net merit index have been proposed that would better account for opportunity cost of genetic progress and penalize cows with low production and longer HL (Schmitt et al., 2019). Therefore, to provide a more inclusive measure for HL or LPL, which can replace longevity and effectively support producers in decision making toward production optimization, it is recommended that HL or LPL also include health- and reproduction-related factors, such as those listed above (e.g., metritis, ketosis, and mastitis, among others), to support balanced management decisions.

Young Stock Rearing and Longevity

Average LPL currently ranges between 2.4 and 3.6 lactations (Doornewaard et al., 2018; Council on Dairy Cattle Breeding, 2019; Lactanet, 2019d), limiting the portion of life during which cows are actually profitable. In fact, as much as 11 to 22% of youngstock are culled before even reaching first calving (Hultgren et

al., 2008; Brickell and Wathes, 2011) and 8 to 19% of cows are culled within the first lactation (Bach, 2011; Brickell and Wathes, 2011), resulting in a financial loss for the producer.

Culling decisions, and thus longevity decisions, are made based on cow health and performance in the lactating herd; however, health, growth, nutrition, and disease during calthood and adolescence have a considerable influence and lasting effect on future health, production, and, therefore, costs (Waltner-Toews et al., 1986; Carvalho et al., 2020). Poor health and nutrition in youngstock reduce growth, incur treatment and labor costs, increase risk of mortality, increase age at first calving, and affect first-lactation milk yield (Shamay et al., 2005; Bach, 2011; Heinrichs and Heinrichs, 2011). Similarly, rearing conditions and youngstock management have a considerable effect on morbidity, reproductive performance, and LPL (Hultgren et al., 2008; Hultgren and Svensson, 2009; Bach, 2011). Yet youngstock data, except for reproductive performance, are rarely monitored or recorded (Bach and Ahedo, 2008). Failure to regularly monitor youngstock subsequently results in producers inadequately identifying potential problems before animals have joined the lactating herd, at which point it may be too late to resolve the problem (Bach and Ahedo, 2008).

Youngstock rearing is an important cost center on most dairy farms and can account for as much as 20% of the overall budget (Fetrow, 1988). Consequently, some producers choose to sell calves and buy pregnant heifers or use custom calf-rearing operations (Walker et al., 2012; Kertz et al., 2017), whereas others rear their own young stock, sometimes keeping all female offspring born on farm, resulting in a higher influx in the dairy herd than strictly necessary. This can result in less favorable culling decisions based on a potential abundance of replacement heifers available (Overton and Dhuyvetter, 2020).

After calving and joining the lactating herd, a cow becomes profitable once she reaches her breakeven point, when the debt incurred during rearing is repaid. This point is unique for each cow and determined by a multitude of factors, including age at first calving, milk yield, and length of the dry period. A recent report from the Canadian Dairy Network (2019b) stated that the average cost of rearing Holstein heifers to 24 mo is CA\$2,650 and takes an average of 42 mo of age (1.5 lactations) to repay. However, there is a great deal of variation in the age at which Holsteins repay the debts incurred during rearing. In order for the cow to be profitable, her HL or LPL must be greater than her specific payback breakeven point that typically is reached after 1.5 lactations (Brickell and Wathes, 2011; Canadian Dairy Network, 2019b).

FACTORS AFFECTING LONGEVITY

Genetics

Genetic Trends. Improvements in animal husbandry and genetic selection for milk yield have led to substantial increases in milk production over recent decades. In Canada, the average milk production per cow per year has increased by more than 2,500 kg from 2001 to 2018 (International Committee for Animal Recording, 2019) and total milk production has continuously increased over the past 40 yr, even while the size of the national herd has decreased (Canadian Dairy Information Centre, 2019b,c). This progress is not unique to Canada; similar trends have been documented in the United States and throughout Europe and Australasia as average milk production per cow has steadily increased year over year (Figure 1).

With new genetics resulting in increasing production, negative consequences were noticed in the 1980s with a simultaneous decline in fitness-related traits, such as reproductive success, udder health, and lameness, which led to an increase in premature culling and reduced longevity (Knaus, 2009; Oltenacu and Broom, 2010). An unfavorable relationship between production and fitness has been well established (Simianer et al., 1991; Hansen, 2000) and had led on average to a decline in health and welfare of cows for 2 main reasons.

First, antagonistic genetic correlations exist between milk yield and diseases such as ketosis, ovarian cysts, mastitis, and lameness (Ingvarsen et al., 2003; Heringstad et al., 2007; Pritchard et al., 2013). Additionally, genetic correlation between reproduction and milk yield is similarly antagonistic (Pryce and Veerkamp, 2001; Roxström et al., 2001). High-yielding cows are often bred later in lactation, require more services per conception, experience more days open, and have a longer calving interval than cows with lower milk yields. However, current genetics trends allow for improvement of milk production through a more flattened persistent lactation curve, parallel to improved health parameters. Estimates of genetic correlation between milk yield and longevity, however, have varied (Tsuruta et al., 2005; Tokuhisa et al., 2014; Sasaki et al., 2017), indicating that selection for increased milk yield has indirectly affected longevity by reducing resilience against factors associated with an increased risk of culling (McConnel et al., 2008).

Second, milk yield and fitness have an unfavorable relationship due to the higher metabolic demand experienced by high-yielding cows, particularly during early lactation, which negatively affects their health and survival (Ingvarsen et al., 2003; Oltenacu and Broom, 2010). When cows are in a negative energy balance,

Figure 1. Average milk production (kg) per cow per year in select countries. Data provided by International Committee for Animal Recording (2019), Dairy NZ (2019), and DataGene (2017).

they are more likely to experience a higher incidence of metabolic disorders and a reduced body condition that can result in reduced reproductive performance and, ultimately, reduced longevity (Bauman and Currie, 1980; Rauw et al., 1998; Walsh et al., 2011). As higher yielding cows are genetically predisposed to allocate more energy to production, intentional breeding for higher production further exacerbates this energy imbalance and leads indirectly to increased culling (Essl, 1998; Oltenacu and Broom, 2010).

Genetic Selection for Longevity. Longer longevity reflected by greater HL and LPL is perceived favorable. Therefore, extensive research has been conducted to study the genetic selection for improved longevity (Vollema and Groen, 1996; Jairath et al., 1998; Sewalem et al., 2005a). This research, however, has not resulted in great effect on HL or LPL for several reasons.

First, a cow's true longevity cannot be known until a culling decision has been made, at which point breeding decisions for this cow can no longer be made. Also, it is not practical to wait until daughters have been culled before a sire's breeding value can be established. Therefore, breeding values are often calculated using survival analysis based on daughter survival or genomic information of daughters on HL or LPL (Ducrocq et al., 1988b). This approach allows for the inclusion of censored records for cows still alive at the time of analysis, represented as the lowest possible boundary of their longevity (Ducrocq et al., 1988a; Essl, 1998). Subsequently, many countries have long shifted away from primarily selecting for production to incorporating traits related to durability (longevity, body size, overall udder, feet and legs, final score, other conforma-

tion traits, milking temperament, and meat quality) and health and reproduction into selection decisions (Miglior et al., 2005, 2017).

Second, longevity as a genetic trait is reported to be lowly heritable worldwide (Madgwick and Goddard, 1989; Vollema and Groen, 1996; Sewalem et al., 2005b). Heritability estimates have ranged between 0.03 and 0.10 when measuring longevity as LPL and between 0.01 and 0.06 when measuring it as a stayability trait (Shabalina et al., 2020). Similarly, the heritability of LPL was found to be low (0.002 to 0.031) when measured in intervals of 1, 3, 6, and 12 mo after first calving; however, these estimates did increase (0.115 and 0.149) when measured as a single 72-mo period after first calving (van Pelt et al., 2015). Heritability estimates below 0.15 are considered to be low, and direct selection for these traits results in slow genetic improvements because realized longevity (without the use of predictions or genomic information) becomes available only at the end of the cow's productive life (Cassell, 2009). Therefore, direct selection for longevity is less effective than selecting for more heritable traits. Consequently, type traits, such as conformation, health, and reproduction-related traits, have been used instead as indirect selectors for longevity (Essl, 1998; Sewalem et al., 2005b; Miglior et al., 2017), resulting in multitrait evaluations that combine direct and indirect measures that have improved genetic selection for longevity (Miglior et al., 2017).

The EBV for longevity have increased over time (García-Ruiz et al., 2016; Council on Dairy Cattle Breeding, 2019). Improvements in the time cows spend in the herd have, however, been limited (De Vries, 2017;

Council on Dairy Cattle Breeding, 2019), even after implementation of genomic testing to select sires. This genetic gain in longevity will likely improve further as genomic testing of females also becomes more widely implemented, allowing producers to make informed breeding decisions earlier in life (Weigel et al., 2017). Additionally, once a cow is born, her genetic composition is set and cannot be changed, but it is optimized management allowing her to be productive to her full genetic potential. Therefore, making changes to breeding programs will have no effect on the longevity of cows currently in the herd (Weigel et al., 2017).

Environment

Cow performance or phenotype is determined through a combination of genotype, the inherited genetic composition that determines biological characteristics, and how those biological characteristics interact with the environment (McConnel et al., 2008; Walsh et al., 2011). Culling decisions, and thereby longevity, are determined based on cow performance; therefore, because the heritability of longevity is low, the environment plays a large role (McConnel et al., 2008). A cow is more likely to avoid culling by being better suited for her environment, indicating that environment is fundamental in determining cow longevity (Tokuhisa et al., 2014). Current housing and environmental conditions of cows, however, are vastly different than their original habitats, and these seemingly “unnatural” conditions have been suggested as a contributing factor affecting longevity (Tokuhisa et al., 2014).

Cattle are grazing animals whose original habitat consisted of open forest or meadows. However, dairy facilities have largely shifted toward housing cows indoors rather than on pasture. Confined housing is often a concern with regards to animal welfare in that it reduces access to natural sunlight and fresh air and restricts the natural movement or behaviors of cows (Fraser, 2008; von Keyserlingk et al., 2009). However, it is also a concern regarding longevity.

Health disorders, such as lameness and mastitis, have a significant effect on milk production (Warnick et al., 2001; Seegers et al., 2003), are associated with reduced reproductive performance (Santos et al., 2004; Pinedo et al., 2016) and longevity (Randall et al., 2016; Gussmann et al., 2019; Shabalina et al., 2020), and are considerably affected by environmental factors. For example, flooring type and slipperiness, barn cleanliness and design (i.e., sharp turns), bedding type and quantity, and stall design (i.e., dimensions and base) are environmental risk factors associated with increased odds of lameness (Barker et al., 2010; Solano et al.,

2015). Similarly, stall design, cleanliness, and bedding type are associated with increased risk for teat injury, or mastitis, or both (Barkema et al., 1999a,b; Peeler et al., 2000).

Furthermore, environment can influence changes in genome function and gene expression via epigenetics, the study of heritable changes in gene expression due to chemical variations, rather than changes within the DNA sequence itself (Khatib, 2012; Singh et al., 2012). Environmental factors (e.g., nutrition, stress, disease, and management) can influence methylation and histone modification or exchange within cells, thereby inhibiting or promoting the expression of certain genes (Kiefer, 2007; Singh et al., 2012). A cow's performance, therefore, is not just the product of genes but also of environmental factors, emphasizing the vital role that environment plays in determining performance and LPL.

Management

The lifetime performance of a cow, and ultimately her longevity, is the end result of a series of both herd-level and cow-level decisions made throughout her lifetime (Fetrow et al., 2006), and these decisions will affect each cow differently based on her unique phenotype. The interaction between genotype and environment is largely controlled by management; therefore, producers are integral in determining phenotypic longevity (Alvåsen et al., 2018). If the interaction between genetics and environment adversely affects longevity, it is then the responsibility of the producer to make management changes that remedy the underlying cause (Rushen and de Passillé, 2013). Because many important risk factors are associated with longevity, such as those associated with production, reproduction, and health disorders, a review of specific management factors associated with longevity is outside the scope of this paper. However, it is clear that the adoption of management practices that have improved dairy reproduction, such as hormone-based breeding programs, genetic improvement, and technologies supporting reproduction, have reduced the forced culling of cows (Moore and Hasler, 2017; Overton and Dhuyvetter, 2020).

With regards to longevity, genetic improvements are more likely achievable as a long-term goal, whereas improving environmental conditions via management could be the objective in the short term but always being adjusted based on the genetic makeup of the herd. However, genetic improvements very much rely on the availability of the preferred genetics for the specific circumstances. This was illustrated by Harris and Kolver (2001), who identified North American Holstein-

Friesian genetics as less suitable for the pasture-based environment in New Zealand, and use of these genetics resulted in reduced survival due to poor fertility.

Before producers make changes to management, they must believe that their current situation poses or will pose a problem in the future and feel that they are responsible for implementing a solution (Ritter et al., 2017). Once aware of the problem, producers must have a realistic goal to work toward and feel that the changes they implement will be effective in helping them achieve that goal (Ritter et al., 2017). Therefore, before producers are likely to make changes to management regarding longevity, they must first feel that the longevity of their herd is a concern and that they are both able to and responsible for fixing it.

Additionally, producers must identify the specific areas negatively affecting longevity in their herd and work toward implementing solutions. Benchmarking key areas of herd management against certain standards and regularly evaluating data on current performance or health status to detect unfavorable trends can help identify weaknesses and problem areas that need to be addressed (Forbes, 2000; Bach and Ahedo, 2008). Further, benchmarking tools allow producers to track their progress and the success of any implemented changes as they work toward their goals.

CHANGING LONGEVITY

Over the last decades, dairy production has been transformed by technological advances, changing demographics, economic pressures, and consumer perceptions (Barkema et al., 2015). These changes have had a varied effect on longevity across milk-producing countries in the developed world. However, they have generally resulted in substantial reductions in the longevity of cows (Knaus, 2009).

Policy and Regulations

A cow's longevity is determined by numerous factors, and the unique conditions of each country, and even regions within a country, will influence the producer demographics and industry framework. Different legislation and regulations within a country elicit different management strategies and goals and, therefore, different outcomes (Bergeå, 2007; Frössling and Nöremark, 2016; Ritter et al., 2017). Factors such as import or export restrictions for cattle, international agreements regulating the trade of dairy products, global abolition of the supply management system (except for Canada), processor capacity, and environmental policies, such as those limiting phosphate production, have had a considerable effect on producer decision making regarding

longevity (Klootwijk et al., 2016; Doornewaard et al., 2018).

Another effect is the availability of heifers for replacement. Under strict phosphate limitations such as in the Netherlands, producers will likely reduce the number of female replacement stock to milk more cows, potentially resulting in longer LPL. However, an increase in reproductive performance and the use of sexed semen has also resulted in an increase in replacement heifers available in most advanced dairy economies, thereby replacing older cows from the herd and reducing the LPL (Overton and Dhuyvetter, 2020).

Strict policies on milk quality in parts of the European Union (EU) compared with North America and Australasia (Australia and New Zealand) can also influence the health status of cows, thereby indirectly affecting longevity. For example, the use of the artificial growth hormone recombinant bovine somatotropin (rBST) has been banned in the EU and Canada since the late 1990s due to concerns regarding animal health and welfare (Brinckman, 2000; Turner, 2001). A report by the Scientific Committee on Animal Health and Animal Welfare (1999) recommended that rBST not be used in dairy cattle due to an increased risk of clinical mastitis, lameness, reproductive disorders, and other production-related diseases—factors that also are associated with reduced longevity (Shabalina et al., 2020). Regulatory bans on the use of rBST, therefore, have likely reduced the risk of health disorders and premature culling. In the United States, rBST use at the herd level has been as high as 60% (Brotzman et al., 2015) but is now much lower due to processors banning its use.

Disease Control Programs

Most EU countries have implemented some degree of mandatory disease testing and eradication, effectively controlling or eliminating certain infectious diseases. One well-studied example that decreases longevity, besides Johne's disease, infectious bovine rhinotracheitis, bovine viral diarrhea, and others, is enzootic bovine leukosis (Bartlett et al., 2013). Several European countries have implemented eradication programs, and some countries have successfully controlled or eliminated the disease (EFSA AHAW Panel, 2015; Kuczewski et al., 2019). Conversely, the dairy industry in North America decided that enzootic bovine leukosis did not necessitate control (Bartlett et al., 2014). Consequently, current herd-level prevalence for bovine leukosis virus infection is estimated to be 94 and 78% in the United States and Canada, respectively (Nekouei et al., 2015; LaDronka et al., 2018). Thus, as cows infected with bovine leukosis virus are more likely to leave the herd

before uninfected cows (Bartlett et al., 2013), it would follow that the forced reduction of test-positive animals in the EU had a long-term positive effect on longevity compared with the United States.

Supply Management and Global Milk Prices

Milk price affects longevity by affecting herd economics, herd size, and health and welfare (Barkema et al., 2015). Producers typically respond to declining milk prices by increasing herd size to maintain their income, reducing discretionary costs such as veterinary care, or participating in herd management programs (Barkema et al., 2015). These reactions, however, often negatively affect longevity by diminishing the health, welfare, and performance of individual cows (von Keyserlingk et al., 2009) and increasing the risk of premature culling.

Countries have responded differently to the pressures created by the need to meet production demands. For example, producers in Ireland, Australia, and New Zealand primarily use management-intensive grazing systems and typically focus on remaining profitable by lowering production costs through maximizing milk production per hectare rather than production per cow (Laven and Holmes, 2008).

Canada has maintained a supply management system, whereas other countries have relied on the fluctuating, and often declining, milk prices of the free market (Sinclair et al., 2014; Barkema et al., 2015). Cow longevity in Canada is influenced by its supply-managed production system, as culling decisions are largely affected by producers' abilities to meet quota but not overproduce. Under this system, there is little value for overproducing; therefore, when producers are over quota, they are more likely to cull cows they would have otherwise kept. Similarly, producers struggling to meet their quota are more inclined to keep cows they would otherwise cull as long as they are able to continue producing milk (Ducrocq, 1994; Vollema and Groen, 1996).

Differences in Longevity Among Countries Reporting Trends Available

This section provides longevity data (presented as HL) that are easily accessed online and therefore were selected for inclusion in this review.

Canada. The effect of the above factors on cow longevity in the developed world is noticeable when comparing changes in the longevity of cows over past decades. Overall, the phenotypic trend of longevity in Canada, measured as HL (age at culling), has been primarily negative between 1997 and 2019 despite some noticeable increases between 2008 and 2009 and

between 2016 and 2017. A considerable decline also occurred between 2003 and 2008 that coincides with the discovery of 2 cows infected with bovine spongiform encephalopathy; one was discovered in Canada, and the other originated from Canada but was discovered in the United States (O'Neill, 2005). This internationally infected cow resulted in a border closure and export restrictions on cattle between Canada and the United States. Consequently, Canadian dairy producers could not export animals, a practice they were reliant on, and likely chose to retain heifers in their herds and cull older cows as a result (O'Neill, 2005).

Between 2008 and 2009, average age at culling increased 2 mo from 61.7 to 63.7 mo (Lactanet, 2019d), possibly as a reaction to the introduction of the continuous quota system. Continuous quota allows for greater flexibility in meeting production quotas, as monthly over- and underproduction are accumulated over time and are accounted for in a producer's cumulative quota position (Canadian Dairy Commission, 2009; Alberta Milk, 2019). The change may have influenced producer culling strategies or decision making, resulting in a temporary increase in longevity. The increase in average age at culling also could have been the result of poor forage quality that resulted in Ontario and Québec failing to meet their quotas for 2008–2009 (Canadian Dairy Commission, 2009). In attempts to ensure that the quota was met, producers may have refrained from culling cows, resulting in an increase in longevity during this period. Likewise, a slight increase occurred between 2016 and 2017, which coincides with a 5.6% increase in quota (Canadian Dairy Commission, 2017).

The Netherlands. In the Netherlands, the reported longevity increased steadily from 65.2 mo to 72.1 mo between 2000 and 2008 (Coöperatie CRV, 2019). From 2008 to 2012, however, longevity decreased to 69.7 mo (Coöperatie CRV, 2019), potentially caused by the use of younger cattle due to export restrictions on heifers or due to expansion plans in preparation for the abolition of quotas (Doornewaard et al., 2018). The quota system was abolished in the EU in 2015 (Klootwijk et al., 2016), and longevity in the Netherlands exhibited a slight decrease during that period. Forced culling in connection with the implementation of the phosphate reduction plan (Doornewaard et al., 2018) most likely explains the sharp decline in longevity from 69.7 mo in 2016 to 67.5 mo in 2018 (Coöperatie CRV, 2019). Longevity is expected to increase again because Dutch farmers may milk more cows if they raise fewer replacement heifers.

Sweden. Longevity statistics available for Sweden were somewhat intermittent, resulting in considerable gaps. However, based on the data available, longevity in Sweden appears to have remained relatively stable over

the past several decades (Bergeå et al., 2016; Alvåsen et al., 2018; Swedish Dairy Association, 2019). Longevity reported in Sweden has remained between 60.0 mo and 60.5 mo since 1998 (Swedish Dairy Association, 2019) despite extensive efforts to improve longevity nationally (Bergeå et al., 2016). One possible explanation for this stagnant progress may be producer attitudes toward longevity. Despite agreeing that longevity should increase nationally and in their own herds, producers have not overtly worked to actually improve longevity in their herds (Bergeå et al., 2016).

United States. In the United States, breeding values for productive life as a genetic trait have increased consistently since 1960, yet longevity as measured by LPL decreased steadily between 1960 and 2011 (Figure 2). In 2012, however, the breeding values for productive life began to increase substantially. This increase has been attributed to the rapid adoption of genomic testing in the United States since 2009, which reduced the generational interval between sires and increased the rate of genetic gain (Hutchison et al., 2014; García-Ruiz et al., 2016). However, if the recent increase in realized longevity was the result of genomic testing and genetic improvement, similar trends would be expected in all countries that have used genomics. As this has not been the case, it is unlikely that the increase in longevity in the United States is the result of genomic testing solely, and therefore the explanation might be the phenotypic increase (Overton and Dhuyvetter, 2020). However, the

time lag of these changes might not be fully measurable yet.

New Zealand. In New Zealand, longevity is measured as survivability (Figure 3). From 1999 to 2006, the proportion of cows surviving to the next lactation was almost identical for the 6 to 7 yr, 7 to 8 yr, and 8 to 9 yr age groups. In 2011–2012, however, the proportion of cows surviving to these older age groups decreased from previous years and has continued to decline in 2014–2015 and 2017–2018. It should be noted that the dairy industry in New Zealand is very sensitive to weather conditions. In 2007–2008, widespread drought caused milk production to decline, and in 2011–2012, favorable pasture growth conditions throughout the season enabled record milk production (LIC, 2012).

Denmark. In contrast to other countries, the average productive lives of cows (reported in days) in Denmark increased from 1990 to 2018 (Figure 4). The productive lives of Jerseys increased only slightly from approximately 1,010 to 1,060 d (SEGES, 2019). Holsteins and Danish Red cows had an average productive life of approximately 825 d in 1990, which increased to approximately 975 d in 2018; however, Jerseys were still retained in the herd longer than the Holstein and Danish Red breeds. Longevity in Denmark remains lower than that in other European countries and is comparable with North American estimates. However, the increase in productive life does indicate positive change.

Figure 2. Genetic and phenotypic trends in the average length of productive life (months from first calving to culling) in the United States between 1960 and 2016. Source: Council on Dairy Cattle Breeding (2019).

Figure 3. Survivability (percentage of cows surviving to the next age group) in New Zealand between 1999 and 2019. Source: Dairy NZ (2019).

MOVING FORWARD

Genetic Improvement Versus LPL

A common argument from dairy producers against increasing HL is that the economic benefits associated with genetic improvement of replacements outweigh those associated with an LPL. Genetic improvement occurs when the genetic merit of a cow is enhanced through selective breeding decisions that result in ge-

netic improvement of the average population (De Vries, 2017). Similarly, genetic lag refers to the difference in genetic merit between different populations; the longer cows remain in the herd (i.e., greater longevity), the greater the genetic lag between the average cow and genetically superior heifers (De Vries, 2017). Subsequently, in attempts to capture genetic improvement, producers cull older cows to make room for genetically superior heifers, thereby increasing annual culling rates and foregoing longevity (De Vries, 2017). Consequently,

Figure 4. The average length of productive life (days from first calving to culling) for Jersey, Holstein, and Danish Red cows in Denmark between 1990 and 2018. Image modified and used with permission from SEGES (2019).

either genetic progress or LPL are compromised by the pursuit of the alternative.

In Canada, the economic value of genetic merit is represented by the Pro\$ index (Canadian Dairy Network, 2019a). The average annual gain in the EBV of Pro\$ can be measured by calculating the difference in average Pro\$ per year, which can then be used to calculate annual genetic opportunity costs. De Vries (2020) provided an example that used annual genetic opportunity costs, depreciation costs, annual cull rate, and average longevity to determine the economic tradeoffs between genetic improvement and longevity in the United States. In this example, the economic benefits of longevity were insensitive to heifer prices and therefore insensitive to genetic improvements in heifers (De Vries, 2017). Instead, the economic benefits of LPL were more dependent on cow depreciation. Ultimately, it was concluded that although genetic improvement is important, it does not warrant sacrificing longevity much (De Vries, 2017). These findings agree with studies concluding that lower culling rates (which result in greater longevity) are more favorable for economic outcomes regardless of whether a quota system is in place (Kristensen, 1989; Bascom and Young, 1998; Groenendaal et al., 2004; Fetrow et al., 2006). An important component to the favorable economic outcomes is the differentiation between forced culling (removing a cow from the herd at a less preferred time) and economic culling, where her replacement will provide a better economic return.

Although lower culling rates result in greater LPL and favorable economic outcomes, culling for genetic improvement is also valuable and should be sought as well. Additionally, the use of genomic testing of females is more widespread, as it provides easy, more accurate identification of desirable traits earlier in life (Weigel et al., 2017). The ability to predict future phenotypes from the foundation for genome-guided herd management and the rate of genetic improvement are expected to increase (Weigel et al., 2017). In the future, therefore, the pursuit of genetic improvement may become more favorable than pursuing LPL; however, genetic improvement may also lead to greater LPL by improving selection for durability and health traits, thereby improving cow resilience. Moreover, little to no information is available regarding the effect of epigenetics on LPL. Further research is necessary to provide insight into the relationships between genetics and the environment and how they affect LPL. A more thorough understanding of this interaction may influence which genetic traits are selected for in the future and could potentially identify better management strategies that will prepare replacement heifers for success. Moving forward, the goal should be to optimize HL and LPL

with cattle reaching their genetic potential in a favorable environment.

Optimizing LPL

It is important to acknowledge that some cows are less efficient milk producers than others and that production efficiency is better served when the LPL of these less efficient cows is shorter. Cows with higher genetic merit, greater production capacity, or better resilience against premature culling are more valuable to dairy producers. These cows should be kept in the herd while less valuable cows are replaced. Hence, a more realistic goal for the dairy industry is to optimize rather than increase longevity or LPL. This can partly be achieved through the use of genomic testing to rear only the heifers with the better genetic makeup as a selective young stock goal. That is, producers should aim to get each cow to reach her phenotypic maximum performance capacity by providing a favorable environment via optimal management so she can achieve her full genetic potential. Once a cow is over her maximum capacity, or marginal value becomes negative, she should be replaced by a cow with greater merit. However, good tools to identify the maximum capacity are not readily available to producers.

By using best management strategies to improve environmental conditions, the underlying causes of forced culling can be addressed, thereby shifting culling decisions from forced to economic culling and simultaneously improving cow welfare (Rushen and de Passillé, 2013). Economic culling decisions increase production efficiency by providing producers the opportunity to retain cows of higher merit in the herd; conversely, forced culling decisions may hinder the herd from achieving its goals (Forbes, 2000). Therefore, aiming to optimize longevity rather than striving to maximize life span will maximize the overall production efficiency of the dairy industry.

Future Effects of LPL

The global dairy industry has undergone considerable changes over the last 30 yr (Barkema et al., 2015) with the introduction of technology and more prominent focus on animal welfare. The industry will continue to develop throughout the coming years, and reasons for pursuing longevity goals will continuously change with time.

Environmental Sustainability. Climate change and environmental sustainability are growing concerns worldwide. Dairy farming is often criticized as a major contributing source of greenhouse gas emissions, for reductions in water quality, and for escalating the de-

mand for increasingly scarce natural resources (Place and Mitloehner, 2010; Grandl et al., 2019). Reducing the number of cows required to produce a given quantity of milk improves environmental sustainability by reducing the carbon footprint per kilogram of milk produced (Garnsworthy, 2004; Grandl et al., 2019). Recently, the effect of methane from cows on global warming potential was shown to be much overestimated in nongrowing populations, and challenges with dairy production-related emissions are constantly evaluated (Allen et al., 2018; Naranjo et al., 2020).

Mature cows have a higher milk yield than younger cows (Langford and Stott, 2012). As a result, greater longevity increases the proportion of high-yield cows in the herd, and fewer cows are needed to sustain a given level of production. However, heifers have a higher genetic potential for milk production. Similarly, the number of replacement heifers required to sustain the herd declines, reducing the amount of inputs consumed and greenhouse gases emitted during a considerable amount of unproductive time (Place and Mitloehner, 2010). Similarly, fewer cows, combined with increased feed efficiency, reduces the demand for land mass, feed, and clean water (Bell et al., 2011; Grandl et al., 2019). Greater HL or LPL, therefore, can also improve the environmental sustainability of dairy farming with management decisions about the optimal number of replacement heifers available (Overton and Dhuyvetter, 2020).

Consumer Perceptions. Consumers have become increasingly vocal about their concerns surrounding environmental sustainability and animal welfare (Graça et al., 2015). Greater longevity is associated with both improved sustainability and animal welfare (Bell et al., 2011; Rushen and de Passillé, 2013) and can therefore be used as a tool to improve consumer perceptions regarding the dairy industry.

Global dairy markets are regulated by consumer demands regardless of the production system (i.e., supply managed quota or free market), and a continued and substantial shift away from the consumption of dairy products would have devastating consequences for the dairy industry. Therefore, ensuring that consumer attitudes toward dairy remain positive is vital to the overall sustainability of the industry, and longevity is a tool that can help ensure continued success.

CONCLUSIONS

Various terms have been used to refer to the amount of time cows remain in the productive herd, resulting in inconsistencies and ambiguities in the definitions of longevity. Adoption of standardized definitions would resolve the current confusion regarding what, specifi-

cally, longevity in dairy cattle refers to. Therefore, it is recommended that LPL (days) refers only to days from first calving to culling, whereas HL (days) should refer only to days from birth to culling. Further, stayability should refer only to a cow's ability to avoid culling and should be measured by the proportion of cows surviving to a specific point in time, referred to as survivability. The HL is determined by a combination of genetics, environment, and management, yet to date the majority of research has predominantly focused on genetic selection for improving LPL, despite its low heritability. Breeding programs are now focused on balanced breeding goals based on selection indices for both productivity and LPL; however, it is integral to continue incorporating durability and health and reproduction into breeding objectives. When longevity measures are applied, economically important performance indicators, such as reproduction, production, health, and youngstock performance, are not currently included in farm-level evaluation of longevity. Incorporation of these factors into future evaluations of HL or LPL would provide a more comprehensive understanding of the conditions of the herd when using LPL as a reflection of performance and a tool for producers when setting farm goals to optimize LPL. Additionally, attention should focus on the role that management plays in determining longevity, and producers should aim to maximize their production efficiency by providing a favorable environment so cows can achieve their full genetic potential. This balanced approach can be achieved by aiming to optimize rather than simply strive for an increase of longer HL.

ACKNOWLEDGMENTS

The authors thank Yvette de Haas (Wageningen University & Research, Wageningen, the Netherlands), who critically appraised the manuscript, and John Kastelic (University of Calgary, Calgary, AB, Canada) for support with editing. Grant-in-aid funded by Alberta Milk, Edmonton, Alberta Canada. UofC file 1042875. The authors have not stated any conflicts of interest.

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