

The effects of breeding and selection on lactation in dairy cattle

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Implications

- Genetic selection to increase milk yield has been very successful.
- Genetic selection can be used to alter the shape of the lactation curve, manufacturing properties of milk, and composition associated with human health.
- Mid-infrared spectral data has potential for enabling low-cost, high-throughput phenotyping.
- There remains a disconnect between farmers' investments in improved milk properties and payment for that milk.

Keywords: Genetic Selection, Estimated Breeding Value, Milk Composition

Introduction

Lactation is a dynamic process of milk production to provide nutrition and immune benefits to the offspring while ensuring maintenance requirements of the mother are met (Darmon, 2009; Strucken et al., 2015). In dairy farming, milk is also the main product marketed for human consumption (Darmon, 2009) which is why farmers have worked to increase milk production over time. Milk production of domesticated dairy cows can reach 30–50 L per day or 6,000 to 12,000 L over a lactation compared to 8–10 L per day and <1,000 L over lactation in feral cows (Webster, 1995). Milk production in cows

follow a dynamic curve starting with an initial rapid increase in milk yield in early lactation (approx. 0–45 days-in-milk, [DIM]), followed by a peak (approx. 46–55 DIM), and then a slow decline in milk yield during late lactation (approx. 56–340 DIM) (Strucken et al., 2015). Factors such as peak milk production, persistency and lactation length determine how the total amount of milk produced is distributed over lactation (Muir, 2004).

Since 1960, the amount of milk produced per cow has almost tripled (Figure 1) which is due in part to genetics (reviewed by Strucken et al., 2015; Miglior et al., 2017; Brito et al., 2021). Selection for production traits in Canada initially focussed on milk yield and milk fat yield (reviewed by Miglior et al., 2017). However, as technology developed also selection started to focus on milk protein yield and the shape of the lactation curve. In particular, the lactation curve, persistency (e.g., persistency of production or rate of decline), week of peak yield and peak yield were considered (reviewed by Miglior et al., 2017). Different milk production traits are now considered in selection indices worldwide to provide a balanced breeding goal where milk production is no longer the sole objective but also includes, for example, health and fertility traits (Miglior et al., 2017; Cole and VanRaden, 2018).

Modelling lactation yield

Total lactation yields.

For the purpose of management decisions and dairy cow genetic evaluations, standardized lactation lengths are used to estimate lactation yield. The International Committee for Animal Recording (ICAR) guidelines for genetic evaluation in dairy cows has standardized lactation length to 305-d (ICAR, 2021), and has adopted guidelines and approved methods for computing 24-h yield and accumulated lactation yield (ICAR, 2022). For example, in Canada the production traits that are used in national indices include 305-d fat yield, 305-d fat percentage, 305-d milk yield, 305-d protein yield, 305-d protein percentage (Oliveira Junior et al., 2021). With most breeding

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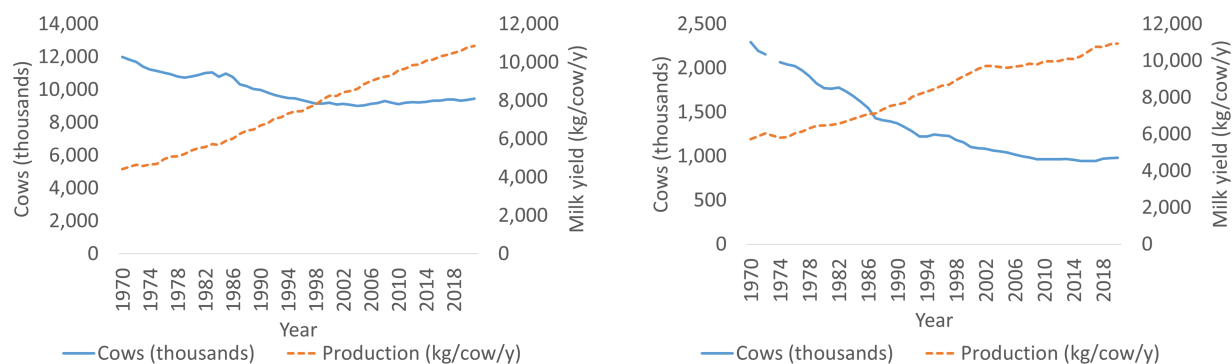


Figure 1. The size of the US (left) and Canadian (right) national dairy herds in millions of cows (left y-axes) and the average milk production per cow in kg/y (right y-axes) between 1970 and 2020 for US and Canadian herds (data from United States Department of Agriculture, Economic Research Service & Agriculture and Agrifood Canada, respectively). Canadian data reflects only animals on herd recording.

values estimated using a 305-day lactation, breeders are making selection decisions based on static values (Strucken et al., 2015).

Genetic evaluation of lactation yield is based on the use of models that incorporate relationships from pedigree information to predict the genetic merits of animals using the best linear unbiased prediction (BLUP). Nowadays, these evaluations use both pedigree and genomic information (i.e., genomic selection) that better accounts for the realized relationships. Lactation yield evaluations were first obtained by analyzing 305-d yields (Voelker, 1981; Pander and Hill, 1993), which were accumulated from the linear interpolation of few weekly or monthly test-day (TD) records (Olori and Galesloot, 1999). Test-day records provide information on daily lactation yield (including milk, fat and protein production) collected from lactating cows by an official milk recording officer. These TD records form the official records of the cows and are usually obtained at monthly intervals through the lactation period; hence, a cow ends up with an average of ten records per lactation. Predicted total lactation yield (305-d) from TD records assumes that the records are representative average of each cows' production in the sampled period, which may not always be the actual case (Swalve, 1995). Therefore, the true yield of a cow might be different from the accumulated 305-d yield predicted from TD records (Anderson et al., 1989). Despite the differences between the true yield and 305-d yield, several statistical methods have been used to model 305-d yield predicted from TD records (Wiggans and Van Vleck, 1979). These statistical models typically treat 305-d yield as a single trait, resulting in relatively simple models with modest computational requirements. The principal drawback of this statistical model is that it only accommodates a common environmental effect associated with all the records despite the fact that different lactation stages (i.e., trimester of lactation) could be subjected to specific environmental effects and it assumes that the lactation curve is constant for all cows (Shanks et al., 1981). However, during the different stages of lactation, a cow's yield can be influenced by metabolic disease, climate variability, feed

changes and stage of pregnancy. Accounting for these specific effects in the model for each individual yield analysis representing the different lactation stages could allow for improved models.

Several authors have suggested the use of a multiple-trait model, in which each lactation record is classified as a different trait (Pander and Hill, 1993; Misztal et al., 2000). Alternatively, lactation records could be considered as repeated record on the same traits and analyzed using a repeatability model (Ptak and Schaeffer, 1993; Swalve, 1995). One of the weaknesses of the repeatability model is that it assumes lactation records collected at different times have a genetic correlation of unity (Jensen, 2001). In addition, for the multiple-trait model where lactations are treated as different traits, the model could be over-parameterized and pose computational challenges. To address the disadvantages presented by the repeatability and multiple-trait models, a random regression model was proposed for longitudinal traits like lactation yield that are modeled by TD records over the course of lactation (Schaeffer and Dekkers, 1994). Random regression models accommodate the structured covariance pattern that exists among the repeated records, adequately adjust for the specific environment effect of the cows over the stages of lactation (using days in milk) and are less over-parameterized when compared to multiple-trait models. The main drawback of this methodology; however, include the large number of records required and the complexity of the models.

Persistency of lactation.

Persistency, which can be measured based on ratios of partial and total yields, variation of yields during lactation or the shape of the lactation curve (Gengler, 1996), could give a more accurate representation of the dynamic nature of the lactation. Furthermore, it has been suggested that cows may benefit from extended lactation lengths to reduce the risk of challenging transition periods (e.g., van Knegsel et al., 2022); cows with a high persistency may be better suited to these longer lactations. Furthermore, with the

increased use of sexed semen resulting in many more female replacements available (>50% of calves born are female in such herds), a rapid turn-around time from lactation to lactation is no longer necessary in nongrazing systems. Longer voluntary waiting periods have been reported to improve overall reproductive success without reducing the number of replacements available (e.g., [Ma et al., 2022](#)). Cows with a high persistency tend to produce less milk than expected in early lactation but more milk than expected during later lactation ([Cole and Null, 2009](#)). Selection for increased persistency could flatten and extend the lactation curve ([Muir et al., 2004](#)), reducing the need to dry off high-producing animals and ultimately reducing the amount of nonproductive time an animal spends in a herd. Consequently, persistency is of economic importance as well as it impacts fertility, health, and feed costs ([Dekkers et al., 1998](#)). Genetic variation in persistency also reduces the accuracy of genetic evaluations for 305-d lactation yield ([Arendonk et al., 1995](#)). However, while genetic evaluations have been developed for lactation persistency, providing separate estimated breeding values for persistency is not common in all countries ([Jamrozik et al., 1997](#); [Cole and VanRaden, 2006](#); [Cole and Null, 2009](#); [Strucken et al., 2015](#)).

According to [Gengler \(1996\)](#), heritabilities for various definitions of persistency range between 0.01 and 0.30. Others have reported heritabilities ranging from 0.09 to 0.30 ([Jamrozik et al., 1998](#); [Muir et al., 2004](#); [Cole and Null, 2009](#)). However, it is important to recognize that not all definitions of persistency have the same interpretation. Test-day models of persistency are typically estimated as the difference in yield between two arbitrary lactation days, one near the peak and one where the lactation curve flattens out in late lactation. If an adjustment for level of production is not made, this can result in high phenotypic and genetic correlations of yield with persistency ([Dekkers et al., 1998](#); [Swalve, 2000](#); [Jakobsen et al., 2003](#); [Muir et al., 2004](#)). This presents a challenge due to the difficulty of altering yield without altering the shape of the lactation curve. [Cole and VanRaden \(2006\)](#) demonstrated that values produced by the best prediction of persistency have low genetic correlations with milk, fat, protein, and somatic cell score and are phenotypically uncorrelated with yield. Selection for milk production later in lactation (changing the shape of the lactation curve) also may provide an opportunity to increase milk production during a time in an animal's life when energy allocation is possible.

Research efforts have focused on predicting lactation curves using different statistical models and, more recently, machine learning approaches ([Silvestre et al., 2006](#); [Ehrlich, 2011](#); [López et al., 2015](#); [Liseune et al., 2021](#)). [Cole et al. \(2009\)](#) reported that it can be challenging to compute curves with satisfactory properties when the number of available records is limited, for example, when working with numerically small breeds or when calculating curves for very specific situations (e.g., breed-parity-region). [Appuhamy et al. \(2009\)](#) showed that persistency is influenced by diseases, such as mastitis, in both the current and successive lactations.

Energy, Metabolism, Milk Composition, Fertility, and Sustainability Traits

Energy and metabolism traits.

Energy is required for lactation and other life functions, including growth, reproduction, and health ([Friggens and Newbold, 2007](#)). These energy requirements and their partitioning changes throughout pregnancy, lactation and return to estrus cycling ([Friggens and Newbold, 2007](#)). During early and peak lactation cows typically experience an energy deficiency as they cannot meet the high energy requirements for milk production because of physiological restraints on feed intake and mobilization of body energy reserves ([Strucken et al., 2015](#)). This negative energy balance can affect large numbers of cows with between 52% and 75% of cows in excessive negative energy balance reported ([Macrae et al., 2019](#)). While there have been improvements in dairy cattle nutrition management ([van Knegsel et al., 2007](#); [Esposito et al., 2014](#)), strong genetic selection on mainly one aspect, lactation, has changed how energy is allocated for other functions ([Friggens and Newbold, 2007](#)). This has led to challenges with metabolic disorders, fertility, immunity, and heat tolerance. These antagonistic relationships between lactation and functional traits have been explained in part by unfavorable genetic correlations, which means that including them in a selection index allows for continued, although slower, genetic progress in milk production, while simultaneously maintaining the resilience of animals ([Pryce and Harris, 2006](#)).

Energy mobilization can be observed in dairy cattle through the recording of an indicator trait, body condition score. In Canada, this score is categorical ranging from 1 to 5, where animals with the lowest score are thin with no fat reserves and animals with the highest score are over-conditioned ([Mongeon et al., 2020](#)). The drop in body condition score is indicative of the mobilization of energy reserves, which can be seen, for example, at the beginning of a lactation period. Several studies have observed that heifers and cows that produced more milk at the beginning of a lactation period, often had larger decreases in body condition scores during this same period ([Pryce and Harris, 2006](#); [Manríquez et al., 2021](#); [Tribout et al., 2022](#)). This rapid mobilization of energy reserves can result in debilitating metabolic disorders in the short-term and have long-term effects on fertility and immunity.

Researchers have investigated the relationship between body condition score and female fertility, finding that genetic selection on higher milk production in early lactation likely exacerbates the already existing negative energy balance, seen in the larger decrease in body condition score, and having a negative effect on fertility ([Van Arendonk et al., 1991](#); [Dechow et al., 2002](#); [Berry et al., 2003](#)). With larger decreases in body condition score and body weight shortly after calving being associated with metabolic disorders, including ketosis, displaced abomasum and metritis, milk fever, ketosis, and fatty liver ([Frigo et al., 2010](#); [Koeck et al., 2012](#); [Stevenson et al., 2020](#)). In addition, higher milk yield was associated with hyperktonemia, and fat and protein production were associated with ketosis and displaced abomasum ([Koeck et al., 2013](#)). Greater body weight and a smaller

change in body weight were favorably genetically correlated with infectious diseases and other diseases (Frigo et al., 2010) and milk yield was unfavorably correlated with ovarian cysts and clinical mastitis (Gernand et al., 2012; Koeck et al., 2014), likely because of the negative energy balance too. Even more far-reaching effects were observed in a study of the effect on females born to mothers lactating while pregnant, where the greater the milk yield of mothers, the larger the negative effects of prenatal programming on milk production, metabolic efficiency and lifespan (González-Recio et al., 2012). Muir et al. (2004) estimated genetic correlations between persistency and reproductive traits that ranged from -0.17 to 0.43 .

Technical properties of milk.

In addition to increasing the overall amount of milk, fat, and protein, selection for desirable milk composition and quality is also possible. Some aspects of this selection are subject to fundamental laws of biochemistry—the osmotic properties required for milk secretion in the alveoli of the mammary gland are fixed—but others are not. For example, many desirable isoforms of milk proteins are under single-gene control (e.g., A2 β -casein), and are associated with both human health and desirable manufacturing properties for cheese. It is also possible to manipulate the fatty acid profile of milk to more closely align it with human nutritional needs (Soyeurt et al., 2009; Knutsen et al., 2022). Finally, milk quality traits, such as somatic cell count, provide an indicator of the quality of the milk, but also the health of the animal, and have been included in most genetic selection programs.

However, phenotyping for advanced traits is often limited by cost, access to appropriate equipment, and throughput. Traditional milk recording programs are based on relatively simple analyses of milk composition: typically, fat content, true protein, lactose, other solids not fat, and somatic cell count. Some milk testing laboratories also have the equipment needed to record mid-infrared (MIR) spectral phenotypes. Precise fatty acid composition typically is determined using gas chromatography, which is expensive and has low throughput. Detailed information about milk protein composition is usually obtained through mass spectroscopy, which has similar limitations. While MIR has been proposed as an indirect phenotype that is low-cost and high-throughput, it often has limited predictive power (Table 1). To overcome these challenges, a small number of direct phenotypes could be combined with a larger number of indirect measurements using bivariate models (Rutten et al., 2011). The use of these tools in breeding programs will allow

breeders to produce more milk and solids with a more desirable distribution of specific characteristics over time. Furthermore, it will allow production of milk that has more desirable properties for both manufacturers and consumers, making selection for peripherally associated traits like reduced methane emissions possible (e.g., Shadpour et al., 2022).

Fertility and reproductive performance.

Genetic selection for improved heifer and cow fertility remains a challenge because the traits commonly used today focus on days open and pregnancy rate (e.g., VanRaden et al., 2004, 2014), both of which have low heritabilities. While these phenotypes are easy to measure on a large-scale basis, they are likely to be poor proxies for the actual biology of fertility. Emerging traits, such as reproductive tract size and position score (Martin et al., 2022), anti-Müllerian hormone levels (Mossa and Ireland, 2019), and endocrine fertility parameters (Tarekegn, 2019), may help produce faster rates of genetic gain than conventional fertility traits because they have higher heritabilities. Bull fertility remains a challenge; many aspects of sperm production do show a genetic component (Butler et al., 2020), but field fertility, commonly measured as conception rate, has a heritability near 0 (Kuhn and Hutchison, 2008). However, correlations of male with female fertility traits also are low, and there is no biologically plausible mechanism by which a cow's lactation performance can directly influence the reproductive performance of her male offspring.

Sustainability and climate change.

Finally, to help mitigate climate change and other emerging challenges, this must also be considered for selection as it has been shown that production selection reduces heat tolerance (e.g., Ravagnolo and Misztal, 2000; Campos et al., 2022) while changes in milk yield, lactation length, or persistency may also alter greenhouse gas emissions (Wall et al., 2012). It might be argued that the ability to resist heat stress is not per se related to sustainability, but there are lots of cows in hot climates that are relatively inefficient, and even modest increases in their ability to breed back and produce good-quality milk may lead to decreases in cattle numbers, reductions in environmental impacts, and increased quality of life for farmers.

Greenhouse gas emissions from ruminants are complex, and are influenced by diet, the rumen microbiome, the host genotype, and interactions among all these systems (Difford et al., 2018).

Table 1. Ability of milk mid-infrared spectra to predict fine milk composition.

Trait	Correlation	Application	Reference
β -Casein proteins	-	Differentiation between A1 and A2 β -casein proteoforms with alleged benefits for human health	Daniloski et al. (2022)
Fatty acids	0.43–0.93	Detailed profiling of milk fatty acids (4:0, 6:0, 8:0, 10:0, 12:0, 14:0, <i>cis</i> -14:1, 16:0, <i>cis</i> -16:1, 17:0, and 18:0)	Maurice-Van Eijndhoven et al. (2013)
Lactoferrin	0.71	Resistance to mastitis	Soyeurt et al. (2012)
Milk acidity	-	Milk acidity is important in cheesemaking (milk coagulation properties, titratable acidity, and pH)	De Marchi et al. (2009)

Table 2. Traits included in US genetic selection indices and the relative emphasis placed on each (1971–2022).

Trait ¹	Relative emphasis on traits (%)											
	PDS (1971)	MFPS (1976)	CYS (1984)	NMS (1994)	NMS (2000)	NMS (2003)	NMS (2006)	NMS (2010)	NMS (2014)	NMS (2017)	NMS (2018)	NMS (2021)
Milk	52	27	-2	6	5	0	0	0	-1	-1	-1	0
Fat	48	46	45	25	21	22	23	19	22	24	27	22
Protein	...	27	53	43	36	33	23	16	20	18	17	17
PL	20	14	11	17	22	19	13	12	15
SCS	-6	-9	-9	-9	-10	-7	-7	-4	-3
UC	7	7	6	7	8	7	7	3
FLC	4	4	3	4	3	3	3	1
BWC	-4	-3	-4	-6	-5	-6	-5	-9
DPR	7	9	11	7	7	7	5
SCE	-2
DCE	-2
CAS	6	5	5	5	5	3
HCR	1	1	1	1
CCR	2	2	2	1
LIV	7	7	4
HTHS	2	2
RFI	-12
EFC	1
HLIV	1

¹Trait abbreviations are: PL = productive life, SCS = somatic cell score, UC = udder composite, FLC = foot and leg composite, BWC = body weight composite, DPR = daughter pregnancy rate, SCE = sire calving ease, DCE = daughter calving ease, CAS = calving ability dollars, HCR = heifer conception rate, CCR = cow conception rate, LIV = cow livability, HTHS = health dollars, RFI = residual feed intake, EFC = early first calving, and HLIV = heifer livability.

²Index abbreviations are: PDS = Predicted Difference Dollars, MFPS = Milk-Fat-Protein Dollars, CYS = Cheese Yield Dollars, NMS1994 = 1994 Lifetime Net Merit, NMS2000 = 2000 Lifetime Net Merit, NMS2003 = 2003 Lifetime Net Merit, NMS2007 = 2007 Lifetime Net Merit, NMS2010 = 2010 Lifetime Net Merit, NMS2014 = 2014 Lifetime Net Merit, NMS2017 = 2017 Lifetime Net Merit, NMS2018 = 2018 Lifetime Net Merit, and NMS2021 = 2021 Lifetime Net Merit.

Methane emissions are highly correlated with milk fat production, so selection for reduced greenhouse emissions is also likely to affect milk composition. This can be addressed through use of uncorrelated phenotypes (Manzanilla-Pech et al., 2021), but it may not be possible through genetics alone to produce high-yielding cows with low total methane emissions. However, the amount of methane emitted by dairy cows per unit of milk, fat, and protein produced continues to decrease. While current discussions are focused on methane because of the ruminant's role in its production, there also may be opportunities to reduce the amount of nitrogen excreted in faeces and urine (Table 2).

Discussion

Breeding goals.

Selection indices continue to evolve rapidly, with focus shifting away from production and fertility towards a broader perspective on cow profitability. Ideally, selection goals should be constructed with input from all sectors of the industry (Cole et al., 2021), but private entities sometimes construct their own indices for commercial exploitation (e.g., Fessenden et al., 2020). However, the milk recording sector has not been as flexible in evolving to meet current needs. Figure 2 shows the flow of information between different sectors in the US milk improvement sector. The portion shaded in blue describes the current providers

and processors of data, but that represents only one source of original data, on-farm testing. As technologies evolve and the value proposition of milk recording changes, genetic evaluation centers will need to be open to accepting data from more sources. An example of such information providers is shown in red, and includes milk processing plants (e.g., manufacturing properties), on-farm systems that do not transmit information to a central database (e.g., automated calf feeders), and farms that do not participate in milk recording programs. While supervised data collection from calibrated meters is the gold standard for milk data, factors can be applied to down-weight records that are collected under less-rigorous schemes.

Novel traits.

Historically, selection for lactation-related traits has focused mostly on milk volume and fat and protein yields, with occasional attention paid to persistency of lactation. This has been very successful, although some challenges have been encountered, principally the antagonism of yield with fertility. Looking forward, however, much more is possible. Progress is being made in developing fertility traits that are closer to actual biology than conception rates or days open, and there are opportunities to produce milk with better manufacturing properties and nutritional properties. However, if farmers are going to breed for traits that

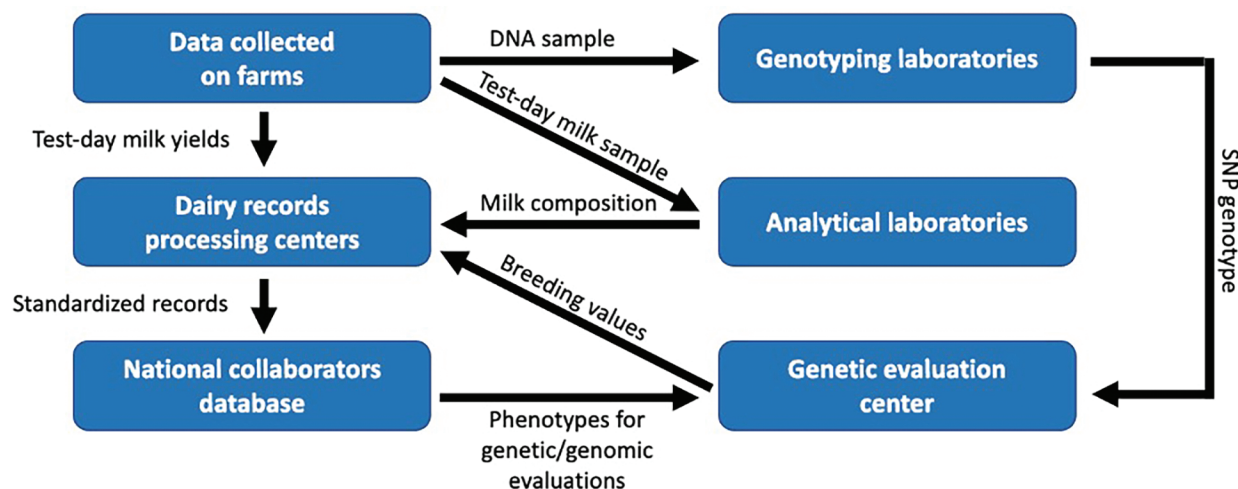


Figure 2. Flow of data between different components of a national milk recording system, including DNA and test-day milk samples collected on farms, milk composition information produced by milk testing laboratories, standardized records computed by dairy records processing centers, and breeding values calculated by the genetic evaluation center.

have added value for the milk processing sector then there needs to be a way for them to capture some of the added value of that milk. This challenge exists around many novel traits, including those that have high recording costs, and it is not reasonable that farmers bear all the cost of data collection while capturing none of the additional value of the milk and its components.

Milk in leading dairy countries is commonly priced on component schemes that consider not only volume but also composition. In many emerging markets, however, farmers are paid only for volume. Regardless of the specific payment scheme used, many emerging schemes for precision management and breeding call for investments in on-farm and milk laboratory equipment (e.g., Koltes et al., 2019). This leads inevitably to the conclusion that there is frequently a disconnect between farmers' investments in improved milk properties and payment for that milk. Growing consumer interest in milk components that are perceived as "healthy", such as the A2 variant of β -casein, has not led to premium payments to farmers; rather, the consumer pays a premium to the process that they capture for themselves. This makes it difficult for farmers to invest in new feed additives, genetics, and other tools because there is no marginal value that they can capture.

Robustness.

It also is important to note that the environment in which the cow is performing, and the management available in that environment, are also crucial factors: high-quality genetics require high-quality management. In this context, management includes all nongenetic aspects of animal husbandry, including housing, feeding, and handling. Most notably, effects of heat stress—which include decreased water and dry matter intake, impaired fertility, and reduced productivity—have been studied for decades (Kadzere et al., 2002). It is also well-established that environmental conditions have life-long effects on animals that begin during gestation (e.g., Cattaneo et al., 2022). It is possible to identify bulls whose daughters can resist the effects of heat stress on milk production (Aguilar et al., 2009),

and some research has focused on robustness in the context of genotype-by-environment (e.g., Collier et al., 1982; De Rensis and Scaramuzzi, 2003; Rauw and Gomez-Raya, 2015), but there are physical limitations that are unlikely to be improved by breeding alone. In particular, to realize the potential of excellent genetics lactating cows must be capable of shedding excess heat, maintaining dry matter and water intake to support lactation, and producing high-quality oocytes to support optimal fertility. Selection for greater robustness can support these goals, but it cannot eliminate the impact of the environment on production. One implication of this is that there is likely no ideal cow for every situation; in the future, genetics will be more closely tailored to the locations in which they'll be used.

Conclusions

Genetic selection to increase milk yield has been very successful, and there is no reason to believe that selection limits are being reached. While most selection has focused on improving yield, there are also opportunities for changing the shapes of lactation curves, manufacturing properties of milk, and composition associated with human health. Mid-infrared spectral data has potential for enabling low-cost, high-throughput phenotyping, and new genetic evaluations based on that technology are now entering the market. However, there remains a disconnect between farmers' investments in improved milk properties and payment for that milk that may limit the potential of these new tools.

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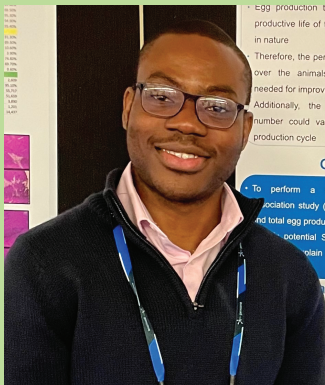
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