Applied Animal Science 38:660–670
https://doi.org/10.15232/aas.2022-02306

SUSTAINABILITY AND INTEGRATED SYSTEMS: *Symposium Article*

Invited Review: Genetic decision tools for increasing cow efficiency and sustainability in forage-based beef systems*

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ABSTRACT

Purpose: The beef industry is experiencing pressure to increase the efficiency and sustainability of forage-based cow-calf production. Dozens of traits affect a cow's ability to be biologically, economically, and environmentally efficient. Furthermore, in an increasingly volatile climate, an animal's genetic merit must be considered in the context of its environment. This review discusses the complex problem of cow efficiency and how the industry can leverage genetic selection tools to improve these traits. I review currently available selection tools for increasing cow-calf production efficiency and discuss developing technologies and research that will drive future innovation.

Sources: This review draws on primary literature from animal breeding, beef production, engineering, and agricultural sustainability to broadly discuss the challenges of genetically improving cow-calf efficiency and adaptability.

Synthesis: Decision support tools allow breeders to select sires that will have more efficient daughters. Historically, these tools have focused on moderating mature cow size and milk production. They have recently expanded to include traits that directly measure feed efficiency and other related phenotypes such as longevity and fertility. Genetic selection tools also exist for adaptive traits to help producers select sires that produce offspring that respond better to environmental stressors such as heat stress or high elevation.

Conclusions and Applications: Future work to develop genetic selection tools for forage-based beef systems will rely on integrating genomics, animal breeding, and precision livestock technologies. These developing technologies, coupled with existing tools, will enable producers to more directly make breeding decisions focused on cow efficiency and greenhouse gas emissions.

Key words: genomics, cow-calf, methane, fertility, novel phenotypes

INTRODUCTION

The beef industry faces pressure from consumers, governments, and nonprofit groups to increase its efficiency and sustainability. Though beef production already has a modest environmental footprint (Gerber et al., 2013; Liu et al., 2021), there are still opportunities for further improvement. Red meat production on a per-cow basis has been steadily increasing since the 1980s (USDA-Economic Research Service). Much of this progress has occurred through postweaning improvements to nutrition and management (Cooprider et al., 2011; Duffield et al., 2012). For this reason, improvements in the cow-calf sector could generate substantial increases in industry-wide economic and environmental sustainability.

Cow-calf production occupies an essential niche, converting low-quality, human-inedible forage into high-quality protein. A growing body of literature exists that suggests that beef production in the context of a well-managed grazing system may actually be climate neutral (Place and Mitloehner, 2021), particularly when methane's role as a "flow" gas is appropriately accounted for (Allen et al., 2018). It is also worth noting that the industry's environmental impact should be viewed as emissions efficiency, a function of emissions and production, as opposed to gross emissions alone. Assuming that beef demand holds steady, shifting production from emissions-efficient systems (i.e., the United States) to less efficient ones (e.g., South America) would only worsen cattle-driven emissions (Dumortier et al., 2012).

Despite the relatively modest portion of greenhouse gases (**GHG**) originating from cattle production, cow-

The author has not declared any conflicts of interest.

*This article resulted from the presentation given at the Bill E. Kunkle Interdisciplinary Beef Symposium, "Forage-Based Beef Management Tools and Their Impacts on Environmental Sustainability," Southern Section of ASAS Annual Meeting, January 2022 in Ft. Worth, Texas.

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calf production is responsible for most of the beef sector's emissions (Rotz et al., 2019). A cow's lifetime GHG emissions are many times larger than a terminal steer's. Not only does a cow live and emit for multiple years, but emissions on forage are significantly greater than on concentrate diets (Aguerre et al., 2011). This longevity also means that the inefficiencies of a cow compound the longer it remains in a herd. Strategies that increase cow efficiency can further reduce the industry's environmental footprint and make beef operations more profitable. Improving cow efficiency and sustainability is a multifaceted challenge, providing multiple avenues for improvement. These could come from direct interventions to increase forage-use efficiency or decrease GHG emissions. Other traits such as fertility, longevity, and animal health can also affect the overall sustainability of cow-calf production.

Many promising interventions exist to decrease emissions, increase cow efficiency, or mitigate environmental stressors. These may come in the form of dietary additives (Almeida et al., 2021), novel forage combinations (Archimède et al., 2011), reproductive management strategies (Fontes et al., 2020), and precision livestock management (Tullo et al., 2019). Although individual animal interventions are promising, their persistence is limited. These are typically restricted to a feeding period or, at most, an animal's lifetime. Other systems-level management solutions have been identified by life cycle analyses that can reduce operations' environmental footprint (Lupo et al., 2013; Asem-Hiablie et al., 2019). In the future, we will rely on the immediate results of interventions, systemic improvements to correct ranch-level inefficiencies, as well as lasting genetic progress for reducing GHG emissions. This review will focus on the latter of these 3 approaches.

Most traits associated with cow efficiency and sustainability are heritable, meaning genetic selection can drive sustained long-term progress. Here, I review existing genetic and genomic tools available to beef cow-calf producers for breeding more efficient animals in forage-based systems. I also highlight emerging technologies that will further enable selection for novel efficiency and sustainability phenotypes. Finally, I discuss potential barriers to implementing and adopting these technologies.

COW EFFICIENCY

Definitions and Component Traits of Cow Efficiency

Efficiency in cow-calf systems can take multiple forms, from metabolic efficiency to feed efficiency to production efficiency to economic efficiency. We can view sustainability through a similar lens, from raw per-animal emissions to emission intensities to the economic sustainability of the industry. Each of these measures of efficiency and sustainability are related but not perfectly aligned.

Cow efficiency and sustainability are compound phenotypes that include direct and indirect component traits. Historically, cow efficiency has been measured in the context of weaned calf kilograms to feed intake or energy requirements on a per-cow basis (Dinkel and Brown, 1978). The chief goal of a cow-calf operation is to maximize the amount of end product (i.e., weaned calf, fat cattle, or red meat) produced per unit of forage resources. For cows, this efficiency is a function of the feed needed to meet basic maintenance needs, coupled with their energy requirements for milk production, reproduction, and coping with environmental stress (Nielsen et al., 2013). In mature cows, over half of dietary energy expenditures are partitioned toward body maintenance functions (Kenny et al., 2018), making it an ideal target for genetic selection.

The beef industry has understood the importance of feed efficiency for decades (Koch et al., 1963), but characterizing the feed intake of grazing cows remains challenging. Feed efficiency can be measured in multiple ways, but the most common in the beef industry are DMI (a raw measure of intake), residual feed intake (**RFI**, deviation of actual intake from expected intake), and residual ADG (**RADG**, deviation of ADG while holding intake constant). All of these traits are related and tend to be moderately heritable. A large meta-analysis by Berry and Crowley (2013) estimated that RFI had a heritability of 0.33 in growing cattle. Feed efficiency in dairy cows was substantially lower ($h^2 = 0.06$), though they noted that measuring feed efficiency in beef cows where milk yield is not measured is more complicated.

Wide-scale feed efficiency phenotyping efforts have typically focused on growing cattle consuming high-energy rations (Berry and Crowley, 2013; Kenny et al., 2018). Measuring forage-based feed intake requires a tradeoff in throughput (i.e., grazing enclosures/forage harvests) or accurate representation of grazing behaviors (i.e., feeding forage in feed intake systems). Furthermore, Meyer et al. (2008) observed no significant difference in grazing intake among high- and low-RFI cows as determined by a previous forage feeding trial. Despite its critical importance to production and economic efficiency, the industry still lacks reliable indicator traits for forage-based feed intake and efficiency. Still, there are multiple imperfect but correlated indicator traits that can be used to approximate forage-based efficiency.

Mature BW has long been used as a straightforward and correlated measure of cow efficiency (Dickerson, 1978). Metabolic BW (**$BW^{0.75}$**) is typically used in place of BW as it is directly proportional to an animal's energy expenditure (National Academies of Sciences, Engineering, and Medicine, 2016). Multiple studies have estimated moderate negative genetic correlations between RFI and mature BW (Archer et al., 2002; Berry and Crowley, 2013). Nevertheless, forage intake and BW are not perfectly correlated, creating an opportunity for successful multitrait selection (Lalman et al., 2022). Antagonistic genetic correlations can also complicate selection procedures as producers attempt to maximize the productivity per unit of feed or forage. Increased selection for calf growth and milk can antagonistically affect the energy requirements needed to sustain those production levels. Single trait selection for feed efficiency may produce later-maturing females, delaying their age at first calving (Crowley et al., 2011).

In addition to BW, we have long understood that when comparing 2 equivalently sized lactating cows, the one with greater milk production will have substantially greater maintenance requirements (Ferrell and Jenkins, 1985; Montaño-Bermudez et al., 1990). Although larger cows wean heavier calves, their additional resource costs may make them less profitable depending on resource availability (Doye and Lalman, 2011). Smaller cows with less milk tend to be more efficient in low-nutrient environments. Conversely, when resources are plentiful, a larger cow may be more efficient at converting energy inputs into weaned calf weight (Jenkins and Ferrell, 1994).

Cow size is a classic example of biology intersecting with the economic and environmental realities of beef production. This is an optimization challenge that lacks a single blanket recommendation. Recent works with bioeconomic models address this optimization problem by integrating knowledge of economic drivers with the biology of cow size, metabolism, milk production, and other economically relevant traits (Pang et al., 1999; Bir et al., 2018; Aherin, 2020). These models allow researchers to explore a variety of parameters to identify optimal management and breeding strategies for operations in specific production environments. Bioeconomic models can assist producers in designing breeding objectives that will maximize economic efficiency in their particular environment and management regimen.

Beyond feed efficiency, there is increasing interest in including enteric GHG emissions in beef breeding and management objectives (Wall et al., 2010; de Haas et al., 2017; González-Recio et al., 2020). This interest is further driven by government mandates and economic incentives for integrating climate-smart production practices. Across beef and dairy cattle, methane emissions are lowly to moderately heritable ($h^2 = 0.09$–0.29; Hayes et al., 2016b; Lassen and Løvendahl, 2016; Brito et al., 2018). These heritabilities suggest that sufficient variation exists to make genetic progress on per-animal methane emissions. Greenhouse gas emissions are favorably correlated, phenotypically and genetically, with feed efficiency (Hegarty et al., 2007; Jones et al., 2011; Manafiazar et al., 2020). These trends appear to persist across diet types. Two small studies have pointed toward favorable phenotypic correlations between RFI and GHG emissions in both cows and heifers fed low-quality unprocessed grass diets (Briggs et al., 2022; Moore et al., 2022). This favorable relationship means that future breeding goals focused on selecting more sustainable cattle will not have to sacrifice cow efficiency for reduced emissions.

In addition to phenotypes directly involved in energy metabolism, many other traits affect an individual animal's overall efficiency and environmental footprint, especially fertility and cow longevity. Whether in a dairy or beef operation, open cows and developing heifers consume resources and emit greenhouse gases while failing to contribute to an operation's end product (Wall et al., 2010). Work by Boyer and colleagues (Boyer et al., 2020) quantified the economic cost of a missed calf. Cows that missed even a single calf had less than a 50% chance of being profitable over an 11-yr productive life. This likelihood fell to 25% for cows that missed 2 calves. Long-lived females are essential for commercial cow-calf profitability. Developing heifers do not contribute to a herd's revenue and consume extensive resources when developed appropriately (Boyer et al., 2018). Beyond economic savings, long-lived cows positively affect the environmental footprint of a herd. In dairy herds, replacement females contribute between 20 and 33% of a herd's total methane emission (Garnsworthy, 2004; Knapp et al., 2014). Modeling by Garnsworthy (2004) estimated that fertility improvements had the potential to reduce herd-level methane emissions by over 10%. The lower replacement rate in beef cattle compared with dairy likely means that this reduction would be smaller in beef herds. Nevertheless, fertility and cow longevity traits enormously affect beef herds' economic and environmental sustainability.

Crossbreeding is one of the most easily implemented tools for increasing the efficiency of forage-based cow-calf production. Despite the clear effects of heterosis across traits (Cundiff et al., 1974; Gregory et al., 1991; Schiermiester et al., 2015), it is vastly under-used in the beef industry (USDA-APHIS, 2008). Work by Andresen and colleagues (Andresen et al., 2020) showed that Hereford × Angus females produced significantly more milk than their purebred Angus counterparts while having lower intake on low-quality forage. Furthermore, the degree of heterosis is inversely related to the heritability of a trait. This means that for the lowly heritable traits that affect cow efficiency (e.g., fertility and health), heterosis can generate massive improvements (Basarab et al., 2018). Heterosis affects each trait involved in cow efficiency and sustainability. As a result, the widespread adoption of crossbreeding programs could be one of the single most effective strategies for increasing emissions efficiency industry wide.

SELECTION TOOLS

Breeding Value–Based Selection Tools

For heritable traits, performing selection based on statistical estimates of an animal's genetic merit is more accurate than phenotypic selection. These EBV enable predictions of an animal's genetic potential for lowly heritable traits or for traits that are not expressed until later in life, making phenotypic selection difficult or impossible (Henderson, 1977). Accurate EBV calculation relies on large numbers of phenotypic records on groups of animals raised in shared environments (contemporary groups; Wray et al., 2019). Recent developments have integrated genomic information into these calculations, resulting in substantial increases in accuracy on animals with few progeny records (Meuwissen et al., 2001; Forni et al., 2011). Selecting sires that will produce efficient daughters is difficult or impossible using phenotypic selection. The economically relevant trait often is not expressed until a candidate's daughter is a mature cow, which could be 4 to 6 yr after sire selection. Identifying sires with favorable genetic potential for daughter efficiency is more effective when using EBV-based selection tools. Genomically enhanced EBV accelerate this process by adding accuracy to predictions for young, unproven animals. This added accuracy reduces generation intervals and generates more rapid genetic progress (García-Ruiz et al., 2016). Genomics are even more critical for traits with relatively few records in a genetic evaluation, an essential consideration as we consider the development of new and novel phenotypes.

Future cow efficiency and sustainability innovations will rely on this same general formula for developing genetic predictions. Genetic prediction machinery is largely established and stable (Misztal, 2016), but new phenotypes representing novel cow efficiency and sustainability measures are needed. Only once these phenotypes are measured on a sufficiently large population of animals containing sizable contemporary groups are production-level selection tools possible (Visscher and Goddard, 1993; Garrick, 2011). The present challenge is not that our genomics machinery is limited but rather that informative indicators for efficiency traits can be difficult or expensive to measure at the population scale.

Existing Selection Tools

Beef cattle breed associations report genetic predictions as EPD, which are equal to one-half of an estimated EBV (Schaeffer, 2019). They represent 50% of the total genetic potential of a sire (i.e., only the fraction of its true breeding value that can be passed on to offspring). United States beef cattle breed associations report multiple genetic predictions directly related to cow efficiency. A summary of many of these measures is reported in Table 1.

These EPD represent direct genetic predictions for many of the economically relevant efficiency traits mentioned previously, especially for feed efficiency, cow size (weight and height), milk production, and fertility. Multiple traits related to feed efficiency have EPD reported, including RADG, DMI, and RFI. Whereas DMI considers only intake-related phenotypes, RADG EPD use information from an animal's postweaning gain, ultrasound fat measurements, and DMI to estimate daily weight gain assuming a consistent amount of feed (Northcutt and Bowerman, 2010; Nielsen et al., 2013). These measures of feed efficiency are based on growing cattle consuming high-concentrate diets. As such, using these EPD, especially RADG or RFI, to select cows with reduced maintenance requirements may have limited usefulness. Multiple breed associations also report a DMI EPD. Because DMI is strictly a measure of intake, this EPD is most useful for integrating feed efficiency into a selection index. When appropriately weighted in an index, DMI EPD contribute the same information as an RFI or RADG regarding feed efficiency (BIF Guidelines Wiki contributors, 2021).

Historical selection for increased growth and performance has led to increased mature cow sizes across production environments (Jenkins and Ferrell, 2006). Modeling by Bir and colleagues (Bir et al., 2018) suggested that smaller cows (431 kg, 950 pounds) would likely be more profitable in southern plains production environments. These production environment–specific optima are likely to vary across the country. Mature weight is highly heritable (h^2 = 0.53–0.59; Kaps et al., 1999; Zimmermann et al., 2021) and not perfectly correlated with calf weaning weight (r_g = 0.66–0.72, where r_g = genetic correlation; Costa et al., 2011). This means that genetic progress can be achieved for decreased maternal weight without sacrificing weaned calf weight. Multiple breeds report EPD for mature cow size. A related phenotype, maintenance energy, is also reported by the Red Angus Association of America (Evans et al., 2002). Maintenance energy is simply the amount of energy needed by an animal to maintain its weight. This does not include the energy required for lactation, pregnancy maintenance, or thermoregulation.

Compared with dairy, beef cattle have a limited genetic selection toolbox for identifying sires that will produce fertile and long-lived daughters. This is primarily driven by the lack of unbiased breeding record reporting. Fertility and longevity traits are typically lowly heritable and often not expressed until later in an animal's life, making EPD-based selection tools essential for genetic improvement. Breed associations report 4 main measures of longevity and fertility. The all-encompassing measure is stayability (STAY), the likelihood a bull's daughter will remain in the herd to age 6 without missing a calf. Stayability accounts for all of the reasons a cow might leave the herd early (fertility, structural soundness, disposition, udder structure, and so on; Snelling et al., 1994; Snelling et al., 1995). Two other direct fertility measures indicate the likelihood a bull's daughters will conceive as heifers (heifer pregnancy, HP), in the first 30 d as second-calf heifers (pregnant 30, PG30), or repeatedly after their first calf (sustained cow fertility, SCF; MacNeil and Vukasinovic, 2011).

Selection Indexes and Sustainability

As with other breeding goals, balancing the multiple component traits of cow efficiency can be a convoluted process for producers. For multitrait breeding goals, combining multiple traits into a selection index can balance the relative importance of a trait and account for genetic correlations (Hazel, 1943). Ultimately, selection indexes allow producers to base selection decisions on a single aggregate value, usually for profit, instead of for dozens of

Table 1. The EPD for beef cow efficiency-related phenotypes reported by US breed associations

Trait[1]	EPD[2]	Interpretation[3]	Reference[4]
Mature cow weight	MW	Difference in daughters' weights as mature cows expressed in pounds	(Northcutt and Wilson, 1993)
Mature cow height	MH	Difference in daughters' heights as mature cows expressed in inches	(Northcutt and Wilson, 1993)
DMI	DMI	Difference in offsprings' postweaning feed intakes expressed in pounds per day	(MacNeil et al., 2011)
Residual ADG	RADG	Difference in offsprings' postweaning gains given the same amount of feed expressed in pounds per day	(MacNeil et al., 2011)
Maintenance energy[1]	ME	Difference in offsprings' required maintenance energy expressed in Mcal/mo	(Evans et al., 2002)
Maternal milk	MM or MILK	Difference in daughters' milk production and mothering abilities. Expressed in pounds of calf weaning weight	(Benyshek et al., 1988)
Heifer pregnancy	HP	Difference in the percentage of daughters who conceive and calve when 2 yr old	(Boldt et al., 2018; Giess et al., 2021)
Stayability[1]	STAY	Difference in the percentage of daughters who remain in the herd when 6 yr old without failing to conceive	(Snelling et al., 1994)
Sustained cow fertility	SCF	Difference in percentage of daughters who will have at least *n* calves after successfully calving as a first-calf heifer	(MacNeil and Vukasinovic, 2011)
Early-season hair shedding	HS	Difference in hair scores (based on a 1–5 scale where 1 = slick and 5 = full winter coat)	(Durbin et al., 2020)
Pulmonary arterial pressure	PAP	Difference in pulmonary arterial pressure expressed in millimeters of mercury (mm Hg)	(Speidel et al., 2020)

[1]Name of production EPD at American Angus Association except Maintenance energy and Stayability, which are from the Red Angus Association of America.

[2]Common EPD abbreviation.

[3]Description of EPD, explained as a difference between sires in average offspring performance.

[4]Official publication that describes the development of the EPD.

individual EPD. For improving cow efficiency, sustainability, and adaptability, selection indexes will continue to be critical tools for balancing multiple traits of varying importance that are genetically correlated with one another.

At present, a single cow efficiency index, $Energy ($EN), is reported by the American Angus Association. This index estimates an animal's annual maintenance costs based on a linear combination of mature weight and maternal milk EPD. This value is closely related to the maintenance energy EPD, but that is reported in dollars in energy savings. That said, across all breeds, indexes designed for operations that retain replacement females emphasize fertility, moderate cow size, and moderate milk. Work in the dairy industry has begun to explore the inclusion of GHG emissions in selection indexes (Richardson et al., 2022). Early results suggest that the relative economic weights on animal emissions within these indexes will rely heavily on carbon prices moving forward.

Selection indexes are generalized, making broad assumptions about the genetic makeup, environment, and management of the herd in which they will be implemented. This means that for traits like mature cow weight, where optimal values differ between operations, the index likely is not perfectly modeling the profit functions. Although most indexes tend to be robust (i.e., minimal reranking of selection candidates across production environments and scenarios), the ability to tailor them to specific producer needs is being explored. The iGenDec tool takes user inputs for herd attributes to generate indexes tailored to distinct herds (Spangler, 2021). iGenDec allows producers to upload information on their herd composition, environment, feed costs, and other more granular production data. Then, the program delivers customized indexes based on marketing endpoint and planning horizon.

GENOTYPE-BY-ENVIRONMENT INTERACTIONS

Modeling Genotype-by-Environment Interactions for Cow Efficiency Traits

Cattle production remains primarily extensive compared with most other livestock species. Grazing cows are exposed to the full spectrum of environmental stressors across the United States (Drouillard, 2018). This creates a unique set of challenges for forage-based beef systems tasked with improving efficiency and sustainability across multiple diverse environments. In many cases, the genetic potential for a trait differs depending on the environment in which it is expressed. This is referred to as genotype-by-environment interactions (**G×E**; Falconer, 1952; Dickerson, 1962). Genotype-by-environment interactions are pervasive in beef cattle and can affect the expression of multiple important traits (Butts et al., 1971; Bertrand et al., 1985; Hayes et al., 2016a; Fennewald et al., 2018; Braz et al., 2021). Due to the vast diversity in production environments across the United States, breeding cattle that are well-suited to their location and management can play a major role in determining a herd's overall efficiency.

In the context of breeding, G×E interactions are of chief interest when reranking between selection candidates occurs depending on the environment in which a trait is expressed. Due to modeling challenges, current genetic evaluations do not account for G×E effects. Instead, they assume that all animals are being raised in an average environment. In the future, genetic evaluations could choose to model G×E for a trait as a reaction norm across an environmental gradient (Bradford et al., 2016) or as a separate trait in different production environments (Rowan et al., 2021).

Genotype-by-environment interactions can manifest in multiple forms and to varying degrees. These are reviewed at length by Hayes et al. (2016a). Genotype-by-environment interactions may play a role in many forage-based cow efficiency traits. A study by Fennewald and colleagues (Fennewald et al., 2018) used genetic correlations between regional populations of animals to detect the presence of G×E in stayability phenotypes. Traditionally, genetic correlations between environments <0.80 indicate significant G×E (Falconer, 1952). Fennewald's work found that genetic correlations for stayability in different regions were <0.8 for 29 of their total 36 region pairs. Numerous other studies have explored the presence of G×E in beef cattle in the context of weight gain (pre- and postweaning) using reaction norm models, typically involved with heat stress (Santana et al., 2013; Bradford et al., 2016). Although not precisely cow-related traits, a clear relationship exists between animals' abilities to gain weight and the levels of environmental stress to which they are exposed.

Adaptive Phenotypes

In addition to directly modeling G×E, efforts have been made to measure and predict genetic merit for adaptive traits that allow animals to cope with specific environmental stressors. When these traits are heritable and sufficient genetic variation exists, targeted selection can improve the adaptability of animals over time (Prayaga et al., 2009). While these do not represent the explicit modeling of G×E, improvements to adaptive phenotypes can increase cow efficiency in specific environments as cows can partition more energy toward milk production or maintaining a pregnancy instead of dealing with stressors. For these traits, we would expect correlated increases in other phenotypes to be restricted to the environment where the adaptive trait provides benefit. Only 2 adaptive traits currently have EPD reported in National Cattle Evaluations: pulmonary arterial pressure (**PAP**) and hair shedding score (**HS**), both by the American Angus Association.

Animals raised at high altitudes are susceptible to high mountain disease or "brisket disease." This condition is caused by pulmonary arterial hypertension stemming from hypoxia at high altitudes (Rhodes, 2005). A test for PAP serves as an indicator for identifying animals susceptible to high mountain disease (Holt and Callan, 2007). This test helps inform culling decisions in high-altitude herds. Untested animals, especially outside AI sires, can create issues without knowing their potential to transmit favorable or unfavorable adaptive genetics to their progeny. Coupled with the moderate heritability of PAP (h^2 = 0.29–0.34; Pauling et al., 2018), EPD-based decision tools are helpful for cow-calf and seedstock operations at high elevations (https://www.angus.org/Nce/Definitions).

For cattle in heat- or fescue-stressed environments, early-season hair shedding is an indicator of an animal's ability to thermoregulate appropriately. Cows that shed their winter coat late in the season cannot properly partition energy toward milk production, leading to decreased calf performance (Durbin et al., 2020). The hair score phenotype is scored annually on a 1 (completely slick) to 5 (full winter coat) scale (Gray et al., 2011). Durbin et al. (2020) found that lower hair scores were genetically correlated with greater maternal weaning weights (r_g = −0.19, where r_g = genetic correlation), an example of how adaptive phenotypes can affect other seemingly unrelated cow efficiency traits. Effects of cow HS on calf weaning weight were significantly greater when the cow was grazing toxic fescue. Like PAP, hair shedding is moderately heritable (h^2 = 0.34–0.40) and is an additional tool for breeders in the South and Fescue Belt to identify sires likely to make better-adapted daughters. An EPD for early-season hair shedding is currently being delivered to producers by the American Angus Association.

For both PAP and hair shedding, the adaptive EPD is only useful in an environment that experiences the associated stressor (i.e., elevation, and heat or fescue stress, respectively). For example, an operation grazing at an elevation of 100 m would not benefit from selecting a bull with an elite PAP EPD.

NOVEL PHENOTYPING FOR COW EFFICIENCY

New genetic selection tools designed to increase forage-based cow efficiency will almost certainly use existing genetic prediction machinery (i.e., BLUP and genomic BLUP). The advent of methods for efficiently and cheaply monitoring large numbers of individual animals has opened opportunities to develop novel, high-throughput phenotypes (Koltes et al., 2019). Evolutions in hardware (e.g., sensors, cameras), data management, and modeling approaches (e.g., machine learning) have broadened the scope of phenotypes that can be collected, analyzed, and predicted.

GHG Emission Phenotypes

Direct measurements of GHG emissions have largely eluded population-scale phenotyping in the beef industry due to the difficulty and cost of measuring (Egger-Danner et al., 2015; de Haas et al., 2017). Respiration chambers and sulfur hexafluoride (SF_6) tracers (Grainger et al., 2007) can capture this information (Garnsworthy et al., 2019), but their use at a population scale in beef systems presents a major challenge. These and other methane quantification techniques are reviewed at length by Tedeschi et al. (2022). Unlike dairy cattle regularly visiting a milking station daily, accessing forage-based beef cows is more complicated. Devices such as the GreenFeed Pasture System (C-Lock Inc.) allow for the collection of methane (CH_4), carbon dioxide (CO_2), hydrogen (H_2), and oxygen (O_2) gas emission phenotypes in grazing cattle at moderate throughput (Hristov et al., 2015; Coppa et al., 2021). Although these tools are major steps forward in directly measuring GHG emissions in animals' natural environment, they do come with some limitations. GreenFeed systems require extended test periods to generate accurate emission phenotypes, and its throughput is primarily dictated by animal willingness to engage with the device. This is a function of animals' proximity to the device and their behavioral propensity to use it. A study by Arbre et al. (2016) found that cattle needed to be using the GreenFeed for at least 17 d to achieve moderate repeatability ($R = 0.78$) and that repeatability continued increasing until 45 d on test ($R = 0.90$). Other studies have demonstrated lower repeatability and additional challenges in calibration and controlling for background gas presence (Tedeschi et al., 2022). Work on the animal behavior, facility design, and management factors that affect GreenFeed use will be essential for maximizing the promising system's effectiveness.

Methane emissions are likely to be included in future breeding goals across ruminant species looking to decrease their environmental impact (González-Recio et al., 2020). However, methane phenotype collection remains expensive. The average US beef cattle operation cannot afford the technology to collect these phenotypes on their herd. Future selection tool development will require concerted phenotyping efforts by academic institutions and breed associations to develop sufficiently large data sets. The high cost and likely sparsity of records make genomically enhanced EBV even more critical. Research focused on identifying easily measured and correlated indicator traits could accelerate these efforts. Continued innovation in GHG quantification technologies will also affect the industry's ability to build sufficiently sized phenotypic databases to deliver genetic predictions to producers.

Precision Livestock Monitoring Phenotypes

Other developments in sensor technologies allow real-time monitoring of animal data. Accelerometer and temperature sensors have been widely integrated in dairy management programs and offer unique opportunities to develop novel phenotypes in forage-based beef cattle (Robert et al., 2009; Siberski-Cooper and Koltes, 2021). These sensors can detect changes in cattle behavior and activity due to disease (Helwatkar et al., 2020), heat stress (Davison et al., 2020), or estrus (Reith and Hoy, 2018). These offer opportunities to measure more granular fertility phenotypes, variation in thermoregulation, and dozens of other complex phenotypes. In addition to sensors, opportunities exist to directly measure different forage-based efficiency phenotypes, including real-time weight gain (Dagel et al., 2022) and water intake (Ahlberg et al., 2019) with precision livestock farming technologies.

APPLICATIONS

The beef industry is rapidly changing, driven by economic, social, and environmental pressure to increase its efficiency. This is especially true in the cow-calf sector, where enormous potential still exists to breed cattle that more effectively use their resources while holding production levels steady. Genetic improvement in efficiency phenotypes for forage-based cows will play a significant part in this sustained progress. The beef industry relies on producer-driven genetic improvement. Whereas the pork or poultry industries can rapidly deploy decision tools for improving efficiency, the beef industry depends on thousands of producer decisions to move the needle. Many of the necessary tools for increasing forage-based beef production efficiency already exist in the form of EPD for traits such as feed efficiency, mature cow size, and longevity. These allow producers to identify sires more likely to sire efficient daughters and increase the overall productivity of forage-based systems. Other EPD for adaptive phenotypes enable producers to select animals better able to cope with stressful environments such as high elevations (i.e., PAP) or heat and toxic fescue (i.e., HS).

In the future, incentives will likely exist for producers who integrate practices that allow them to decrease resource use (e.g., feed, forage, or water) and GHG emissions. As a result, genetic selection tools for more sustainable animals may further assist producers of all sizes in becoming more economically efficient.

Ensuring that the beef industry remains sustainable economically and environmentally will rely heavily on the cow-calf sector. Novel phenotype development will require cross-disciplinary academic collaborations between geneticists, nutritionists, physiologists, statisticians, data scientists, engineers, and others. Further work with industry partners, producers, and breed associations will be needed to ensure these valuable tools are developed and delivered with the end-user in mind.

ACKNOWLEDGMENTS

T. N. Rowan thanks the Southern Section of the American Society of Animal Science for inviting him to the Kunkle Symposium to discuss the work outlined by this review. This research was supported by USDA National Institute of Food and Agriculture (NIFA) Hatch project S1086 (Enhancing sustainability of beef cattle production in Southern and Central US through genetic improvement) and USDA-NIFA Foundational and Applied Sciences Grant 2022-67015-36214 (Dissecting Molecular Heterosis in Beef Cattle).

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